ISSN 0704-3716

Canadian Translation of Fisheries and Aquatic Sciences

No. 5435

Acanthobdella peledina Grube, 1851

N. Livanow

Original title: *Acanthobdella peledina* Grube, 1851

In: Zoologische Jahrbucher. Anatomie. (Zoological Yearbooks. Anatomy.)
22, 1905-1906, pp 637-866 and plates

Original language: German

Available from:
Canada Institute for Scientific and Technical Information
National Research Council
Ottawa, Ontario, Canada K1A 0S2

1989

273 typescript pages

Secretary of State Secrétariat d'État

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU BUREAU DES TRADUCTIONS

LIBRARY IDENTIFICATION – FICHE SIGNALÉTIQUE

Translated from - Traduction de: German

Into - En: English

Author - Auteur: N. Livanow

Title in English or French – Titre anglais ou français

Acanthobdella peledina Grube, 1851

Title in foreign language (Transliterate foreign characters)
Titre en langue étrangère (Transcrire en caractères romains)

Acanthobdella peledina Grube, 1851

Reference in foreign language (Name of book or publication) in full, transliterate foreign characters.
Référence en langue étrangère (Nom du livre ou publication), au complet, transcrire en caractères romains.

Zoologische Jahrbücher. Anatomie. 22, 1905-1906

Reference in English or French – Référence en anglais ou français

Zoological Yearbooks. Anatomy. 22, 1905-1906

Publisher - Editeur: not shown

Place of Publication
Lieu de publication: not shown

DATE OF PUBLICATION
DATE DE PUBLICATION

Year Année	Volume	Issue No. Numéro
1905/06	22	

Page Numbers in original
Numéros des pages dans l'original: 637-

Number of typed pages
Nombre de pages dactylographiées: 110

Requesting Department
Ministère-Client: DFO

Translation Bureau No.
Notre dossier nº: 3116354

Branch or Division
Direction ou Division: Scientific Publications

Translator (Initials)
Traducteur (Initiales): PH

Person requesting
Demandé par: H. Cameron

NOV 24 1988

Your Number
Votre dossier nº:

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINEE A LA PUBLICATION

Date of Request
Date de la demande: July 4, 1988

Canada

SEC 5-111 (84-10)

Secretary of State Secrétariat d'État

90-00610/

MULTILINGUAL SERVICES DIVISION — DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU BUREAU DES TRADUCTIONS

Client's No.—N° du client	Department — Ministère DFO	Division/Branch — Division/Direction Scientific Publications	City — Ville Ottawa, Ont.
Bureau No.—N° du bureau 3416354	Language — Langue German	Translator (Initials) — Traducteur (Initiales) PH	NOV 24 1988 and Feb 1, 1989

Acanthobdella peledina Grube, 1851

by

N. Livanow

SEC 5-25 (Rev. 82/11)

Canada

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINEE A LA PUBLICATION

Zoologische Jahrbücher. Anatomie. 22, 1905-1906
(Zoological Yearbooks. Anatomy. 22, 1905-1906)

Reprinting prohibited.
Translation rights reserved.

***Acanthobdella peledina* Grube, 1851**

by

N. Livanow

(Institute of Zootomy, University of Kazan)

The present paper is a continuation of the author's *Studies on the morphology of Hirudinea* (1903, 1904)[1], and it presents the results of his observations on the entire organization of *Acanthobdella peledina* Grube.

---

[1] I wish to take this opportunity to correct some typographical errors which have remained uncorrected in my previous paper (1904, 2) on the *Nervous system of the head end and its metamerism*. 1) p. 203, line 7: the word "paramarginal" is to be followed by "ventral and internal paramarginal"; 2) Table 10, Fig. 19: the terms 4 un and 5 un were reversed, and thus the origin of the associated nerves in Fig. 18 also should be corrected.

This interesting worm was described for the first time by E. GRUBE (1851), who obtained it from MIDDENDORFF's Siberian material and provided fairly accurate information about its external morphology. The specimens available to GRUBE had been found in the Yenisei River "on *Salmo peled* Lepech". In 1868, K. KESSLER also collected *Acanthobdella peledina* in Lake Onega on *Salmo salvelinus* L. He also provided a very good description of the external morphology of this species.

Until recently we knew almost nothing about the internal structure of *Acanthobdella*, because GRUBE's descriptions were quite insufficient and in some respect incorrect. (He had "opened a specimen to determine with greater certainty the place occupied by this species among the worms".) Then in 1896, the treatise by A. KOWALEVSKY appeared in which he sketched the entire organization of *Acanthobdella peledina*. However, this was only a preliminary report which was not followed by further detailed studies. As KESSLER had done, KOWALEVSY collected *Acanthobdella peledina* in Lake Onega on *Salmo salvelinus* L. and *Salmo trutta* L.

As far as the species are concerned on which the previous studies were based, the following comment by KOWALEVSKY (1896, p. 273) should be cited here in full: "En me familiarisant d'avantage avec L'*Acanthobdella* du lac d'Onéga, et celle qui était décrite par GRUBE de la collection de M. v. MIDDENDORFF, apporteé du Jénissei, et dont je possède aussi quelques exemplaires du Musée de l'Académie Impérial de Sciences, je trouve que L'*Acanthobdella* du Jénissei et du lac d'Onéga différent l'une de l'autre. Précisément: le bout postérieur du corps chez celle de Jénissei est beaucoup plus étroit que la partie moyenne du corps, tandis que chez celle du lac d'Onéga le passage de la partie large à la partie étroite est beaucoup moins prononcé, ce qui est même assez bien représenté sur les dessins de GRUBE et de KESSLER. Les soies en crochet présentent aussi une certaine différence: chez celle du lac d'Onéga elles sont plus recourbées que chez celle de Jénissei." This indicates that KOWALEVSKY left the question unsanswered whether the acanthobdellids occurring in Lake Onega and those in the Yenisei River belonged to the same or to different species.

In 1900, B. POPPIUS registered the occurrence of *Acanthobdella* in Lappland[1]. At about the same time, E. BRUMPT provided a brief description of the reproductive apparatus of this worm, but did not give details regarding the site where it was found.

All information provided by the above named authors will be fully discussed below.

The author of the present paper collected *Acanthobdella* in the summer of 1902 in Lake Onega near Vytegra, on *Salmo salvelinus* L. Following the example of his predecessors, he refers to the species as *Acanthobdella peledina*, since he is not able to settle the question raised by KOWALEVSKY.

Finally it should be noted that statements, such as those by GERSTÄCKER and CARUS[2], that *Acanthobdella* occur in the Sea of Okhotsk, or by E. PERRIER (1897) who wrote "*A. peledina*, côtes de Sicile"[3], are apparently attributable to errors, as KESSLER (1868) had already pointed out in connection with the former.

The author's methods were those generally used: preservation – primarily in sublimate glacial acetic acid (3:1) and Hermann's fluid –, double-embedded in photoxylin and paraffin, and stained, either *in toto* or in sections, mainly with haemalum, ferrihaemotoxylin, or borax carmine indigo.

1. External morphology

Regarding the dimensions of *Acanthobdella peledina*, GRUBE (1851) wrote as follows: "The most impressive specimens measured 1 inch 1 lin.* in length, 2.3 lin. at the thickest part which was closer to the anterior than to the posterior end, and 0.5 lin. at the posterior end. Another specimen had the same thickness and was 1 inch 3 lin. long, smaller specimens were 9 lin.

---

[1] This fact is known to the author only from the literature cited in the *Zoologischer Anzeiger* (Zoological Bulletin); the treatise itself is not available to him.

[2] Cited according to KESSLER (1868, p. 117).

[3] Probably taken from CLAUS, *Grundzüge der Zoologie* (Principles of Zoology) where Sicily is mistakenly named instead of Siberia as the find spot.

* Translator's note: The values of the old German measurements "Zoll" (inch) and "Linie" (line) differed from region to region. It is therefore not possible to give equivalents in mm.

long, 1.4 lin. at the thickest part, and 0.5 lin. at the posterior end. KESSLER (1868) wrote: "Among the individuals examined by GRUBE were some that reached up to 37.5 mm in length and 5.7 mm in thickness; but the largest of my specimens were only 20 mm long and 3 mm thick". The approximately 100 *Acanthobdella* specimens collected by the author in Lake Onega were all of roughly the same size, reaching a length of up to 30 mm and a thickness of 3 mm in the dormant state.

GRUBE (1851) stated that all individuals he examined were of "round"** shape, "tapered at both ends, a little flattened at the anterior end. In the smaller individuals, the posterior taper was more gradual. Since the trunk of the larger specimens was somewhat more bloated in the middle, they had a sipunculid appearance". The body shape was described by KESSLER (1868)[1]: "At first sight, our individual very much resembles a Hirudinea. Its body is irregularly spindle-shaped, tapering more toward the anterior than the posterior end, so that it is usually thickest in its third quarter. The body tapers very gradually toward the anterior end, while its posterior end sometimes has a cylindrical appearance and recedes in steps from the thickened part ... The anterior end is noticeably flattened, especially on the ventral side". KOWALEVSKY (1896, p. 263) wrote: "Les dessins que nous possédons de l'*Acanthobdella* ont été faits des exemplaires conservés dans l'alcool où l'*Acanthobdella* se contracte de telle manière qu'elle rappelle plutôt un Phascolosome, tandis qu'à létat vivant elle ressemble tellement à une Hirudinée que les pècheurs eux-mèmes la nomment souvent sangsue ... (p. 264): Le dessin coloré de M.A. MOQUIN-TANDON dans sa monographie de la famille des Hirudinées de 1846, tab. 5, No. 1, 2, du genre Aulastome ... rappelle le plus l'aspect général et la couleur de l'*Acanthobdella* vivante et étendue". To these descriptions the author only wishes to add that *Acanthobdella* greatly expands in agitated water, moving the whole body in all directions while remaining attached with the attachment disk, greatly resembling a *Protoclepsis*.

All specimens of GRUBE (1851) were "of pale greyish-yellow colour". KESSLER (1868) wrote: "The colour of our individuals is greyish-brown, but

---

** Translator's note: The German term "drehrund" is an unusual description. It might mean "completely round", "spiral-round", or something else.

[1] KESSLER provided a rather good illustration (Table 6, Fig. 6A) of Acanthobdella, after a preserved specimen.

when preserved in alcohol, they very soon become yellowish-white". KOWALEVSKY (1896, p. 265) stated in this respect: "L'*Acanthobdella* est d'une couleur brun-verdâtre, avec les points jaunes; la partie dorsale est plus colorée que la partie ventrale. La coloration n'est pas uniforme, on voit des raies transversales plus foncées correspondant au nombre des somites". The live *Acanthobdella* observed by the author were grey with a slightly flesh-coloured tinge, and they differed in this respect from those examined by KOWALEVSKY. Furthermore, almost all individuals had 6-7 dark annuli in their anterior body section*. In some, these annuli extended over the whole body, so that they had about 23 dark lateral stripes; but generally the mid body section was of very uniform colour and without dark annuli.

GRUBE (1851) gave the following information about the external annuli of *Acanthobdella*: "In the smaller individuals alone I noticed uniform annuli over the whole body; the annuli were clearly defined, and 80 in number. In the larger individuals, however, annuli were clearly formed only in the anterior and posterior parts, while in the middle they turned into annuli that were traversed by longitudinal stripes, giving the surface there a grid-like appearance". KESSLER (1868) explained: "Altogether I counted up to 94 annuli or body segments (not 80 as stated by GRUBE), but these annuli are neither completely regular nor completely identical. Some also have a lateral furrow that divides them into two often unequal halves". He also claimed in contrast to GRUBE that in all specimens examined by him, the body had "annuli over its whole length, from the anterior to the posterior end". The illustrations of *Acanthobdella* provided by KOWALEVSKY (1896, No. 1, 2 and 3) clearly show annuli over the whole body. In my individuals the annuli were hardly discernable with the naked eye, although they became clear under the magnifying glass. The information provided by GRUBE, which is contrary to all other observations, is inadequate for the reason that he examined individuals which were apparently injured and disfigured. This becomes clear enough by his own description: "For the most part, the outer skin had been detached in bag-like fashion, or it hung from the side like rags".

---

* Translator's note: The author uses the German term *Abschnitt* in a variety of ways, sometimes in the specific sense for somite or segment, sometimes in the general sense for sector, section or part. In this translation, "somite" is used only where the German text reads *Somit*, while the German *Abschnitt* is translated as "sector" or "section". The German *Segment* or *Glied* is always given as "segment", and *Region* as "region".

According to the author's own observations, the whole body of *Acanthobdella* has annuli (Fig. 33, No. 1), although the different annuli of an individual are not equally developed, and their total number varies from one individual to another according to the development of the annuli. We will now examine how the annuli are distributed over the different body sections.

In the further discussion of the external morphology of *Acanthobdella*, the author divides the body into the following 5 regions (Fig. 33, No. 1): 1. head region; 2. clitellar region ("girdle region" with the preclitellar and clitellar somites); 3. midgut region; 4. hindgut region; and 5. attachment disk region. This division is based on the entire factual material provided by the detailed study of internal organization, as will become apparent from the relevant sections of the present paper. By and large the author will retain the division suggested by S. APATHY (1888) for Hirudinea, albeit with certain fairly important deviations in terms of the demarkation of individual body regions and the exclusion of the so-called anal region for whose presence there is insufficient morphological evidence.

GRUBE (1851) wrote as follows about the head region of *Acanthobdella*: "The mouth is situated at the actual anterior end and consists of an extremely small roundish opening of the 1st annulus, standing on the tip of a papilla; there is no anterior attachment disk. To the left and right of the mouth are 2 pairs of hardly discernable barbs above each other, almost evenly distributed over the circumference of the annulus. The same are found on the 2nd, 3rd, 5th and 9th annuli, but here the upper pair is closer to the lateral wall, while the lower pair is closer to the ventral surface ... I question whether they are on the same annuli in all individuals; in some the most posterior were no longer present or may have been absent from the start." KESSLER (1868) provides slightly different information: "The small oval mouth opening is situated dorsally on the 1st annulus, near its anterior edge; but I never noticed that this opening is on a separate papilla, as GRUBE stated. On the 1st annulus, to the left and right of the mouth opening, are 2 pairs of barbs each. Annuli 2, 3, 5, and 9 each also have 4 pairs of barbs, arranged in such a way that they form 2 parallel rows on the ventral part of the body ... The annuli of the trunk which immediately follow the head annulus, are somewhat wider than the others and more or less regularly fused with each other, namely annulus 2 with annulus 3, annulus 3 with annulus 4, 4 with 5, 5 with 6, 6 with 7, 7 with 8, and 8 with 9". Finally we have the statement by KOWALEVSKY (1896, p. 265): "Les auteurs qui ont décrit l'*Acanthobdella* ont donné une déscription assez exacte de leurs soies du bout antérieur du corps, mais personne n'a mentionné l'existence des petites soies de remplacement qu'on trouve à la base des grandes soies, et qui servent sans doute à remplacer les soier usées ou perdues; souvent ces soies s'accroissent et deviennent aussi longues que les autres. Nous trouvons aussi chez l'*Acanthobdella* trois paires d'yeux: une paire au bout antérieur du corps, presque immédiatement sur le ganglion sus-esophagien ... la 2. paire d'yeux est placée sur les côtes, à la base de la troisième paire des soies; la 3. paire, aussi du côte du corps, près de la base de la 5. paire des soies". A closer look at the illustration provided by KOWALEVSKY (No. 3) shows the following: The anterior end consists of a pronounced cephalic lobe (l) of which KOWALEVSKY (p. 268) wrote: "le canal intestinal commence par l'ouverture buccale placée sous un prolongement conique de la tête qui a la forme d'une lèvre supérieure, et conduit dans la cavité buccale". This is followed by the 1st head annulus. On each side of each head annulus are 2 pairs of chaetae, namely the pairs of main chaetae in annuli 1, 3, 5, 8, and 11; the pairs of auxiliary chaetae in annuli 4, 6, 9, and 11. The chaetae protrude from the skin sometimes in the middle of the annulus, sometimes in the dividing furrow that precedes the annulus. Thus annuli 2, 7 and 10 would be without chaetae. In the same illustration the position of the eyes is shown in a similar fashion, but the 2nd pair of eyes is shown adjacent to the chaetae pairs of somite 4, while according to the description it should be adjacent to the chaetae of somite 3. Completely puzzling in this illustration is that the pairs of main and auxiliary chaetae of somites 2, 3 and 4 are shown not in the same annulus, but in two adjacent annuli.

The author's own observations indicate that the head region of *Acanthobdella* consists of 5 somites (Fig. 33, No.1; Fig. 35, No.17). Of these, somite 1 (1) contains only one single annulus and is situated on the ventral side of the head, while only a narrow seam of its anterior section is visible dorsally. Somite 1 forms an almost regular circle in whose centre the mouth opening appears as a small longitudinal slit. Dorsally and laterally the 1st head somite is almost totally covered by the anterior edge of the following 2nd head somite (2); it looks almost as if it were inserted into the latter. In the vicinity of the marginal furrow are 4 pairs of chaetae (Fig. 33, No.1 bs_1; Fig. 35, No.17 bsz_1), which will be discussed below. One of each is situated in the middle of the anterior and posterior quadrants.

A special cephalic lobe is not present; neither was the author able to find GRUBE's papilla which is supposed to contain the mouth opening. It could be that GRUBE mistook a turned-out part of the foregut for such a "papilla", whose existence KESSLER was completely justified in questioning. On the other hand, it seems that KOWALEVSKY regarded the most anterior section of the 1st head somite, which lies anterior of the mouth, as a special extension of the head, although no such extension can in reality be distinguished.

As the 1st, the 2nd head somite (2) is also formed by only one annulus. Because of the the ventral position of the 1st head somite, the ventral section of the 2nd is pushed back, forming an arc at the posterior edge of the 1st, while the dorsal section appears as the most anterior annulus of the head end when seen dorsally; only a very small part of the 1st somite protrudes before the head end. On the ventral intermediate line and at an equal distance from the lateral line, the 2nd head somite has 1 pair of closely adjacent chaetae on each side of its anterior section.

The 3rd head somite (3) consists of 2 well differentiated annuli. Their ventral sections are displaced caudad, but the arc formed by the section is less curved caudad than is the case with the annulus of the 2nd head somite, and less in the 2nd annulus than in the 1st. Ventrally the 1st annulus carries 2 pairs of bristles on each side (Fig. 35, No.17 bxz_3) on the same lines of the body as in the previous somite. On each side of the same annulus a black dot can be seen close to the median line – the 1st pair of eyes (au_1) of *Acanthobdella*, as KOWALEVSKY quite accurately stated. The 1st annulus of the 3rd head somite is clearly separated from the annulus of the 2nd somite; no signs of any fusion – as KESSLER had claimed – could be detected. The 2nd annulus of the 3rd head somite has no special characteristics; it is as clearly separated from the following annulus as from the previous one. KESSLER's suggestion that the 4th and 5th head annuli might be fused can therefore not be confirmed. As far as KOWALEVSKY's illustration is concerned, the author cannot correlate it with his own observations, either in regard to the somites already described or to those whose description follows.

The 4th head somite (4) is composed of 4 annuli, but the 1st annulus seems only dorsally well delineated from the 2nd, while ventrally the differentiation is not very pronounced. That is why GRUBE and KESSLER regarded these two annuli as one, i.e. the 5th head annulus. The 3rd and 4th annuli are just as poorly defined, and that is why KESSLER thought that these annuli (his 6th and 7th) were fused with each other. Only in the anterior annuli can a slight backward shift of the ventral section be observed, while this is hardly possible in the posterior annuli. Ventrally the 2nd annulus of the 4th head somite has 2 pairs of setae on each side along the above mentioned lines, and laterally, in the anterior section almost on the marginal furrow between the 1st and 2nd annuli, is a black dot on each side – the 2nd pair of eyes (au_2) of *Acanthobdella*.

The 5th head somite (5) has 4 annuli, the 1st of which is difficult to distinguish ventrally from the 2nd annulus, and that is why KESSLER was justified in thinking that his 8th and 9th head annuli were fused. The 3rd and 4th annuli are well differentiated, but they still seem somewhat less developed than in the following trunk somites. Thus the chaetae (Fig. 33, No. 1 bs_5: Fig. 35, No. 17 bsz_5) and the eyes – the 3rd pair of eyes (au_3) – are of exactly the same position and development as in the previous head somite, and KOWALEVSKY's conclusions about the eyes of *Acanthobdella* are completely confirmed.

It should be mentioned that while *Acanthobdella* does not have a sucker in the actual sense of the word, there are certain indications that one is beginning to develop. It can be seen that the 5 head somites, which are dorsally arched as usual, are slightly flattened ventrally and sometimes already appear somewhat concave in the middle (Fig. 33, No. 2, 3). We have already cited GRUBE and KESSLER in this connection. However, the anterior end is attached mainly by means of the chaetae which, as we have seen, are arranged in regular longitudinal rows of 2 pairs each along each side of the median line.

All described head annuli except the 3 most anterior ones can show a more or less distinct differentiation in the demarkation of a somite or in one of its halves in that 2 annuli may occur instead of 1, or – conversely – that 2 annuli may fuse to become 1. Even when one takes this phenomenon into account, the above mentioned illustration by KOWALEVSKY (No. 3) cannot be explained. It is very unlikely that he was confronted with another *Acanthobdella* species, particularly since KESSLER's and GRUBE's findings agreed with the author's, except that the eyes of their specimens had disappeared because of storage in alcohol. The auxiliary chaetae which in KOWALEVSKY's diagram were drawn much too large and in a position quite independent of the main chaetae, occur in reality at the base of the completely developed main chaetae. The auxiliary chaetae can be poorly developed or altogether absent, and that is why GRUBE and KESSLER had overlooked them altogether.

Posterior of the last head somite, the ordinary, typically developed trunk somites commence; they each contain 4 annuli, and the number of their annuli is not reduced (Fig. 33, No. 1). The development of the lateral furrows shows a certain graduation of these somites. The furrows between individual somites are always clearly defined, while among the furrows that divide the individual annuli of a somite, the median furrow can be more developed than the anterior or posterior furrows.

Immediately following the head region are 3 preclitellar somites (6-8). In the 1st and 2nd preclitellar somite (6, 7) there is a nephridial opening on the ventral intermediate line of the body on each side between the 1st and 2nd somite annulus (Fig. 33, No. 1 $nph_{6,7}$; No. 4 nph^{*}_{6}). In the 3rd somite (8) only the respective indentations of the main epithelium are present; they sometimes appear to be only unilaterally developed, and sometimes they are absent altogether.

This is followed by 3 clitellar somites (9-11). In connection with the latter, GRUBE (1851) wrote: "In the middle line of the ventral surface are 2 small lateral slits in close succession. In one of the small specimens (all with annuli), I saw the anterior slit on annulus 31, the posterior slit on annulus 32; in the larger specimens counting was more difficult, but the above seemed to be confirmed. The posterior slit had opened further in some, giving the appearance of a real, deep opening that one did not have in the case of the first. On the 27th annulus I also observed a smaller, sometimes roundish opening that is sometimes surrounded by a faint wall. Two of these openings probably correspond to the genital openings in Hirudinea". Based on GRUBE's description, K. DIESING (1858) wrote: "apertura genitalis una sub annulo 31mo, altera sub annulo 32do". As indicated by the foregoing, such an interpretation of GRUBE's findings is incorrect, since the latter had left the question open. KESSLER (1868) also wrote: "Ventrally on the median line, 3 lateral, slit-shaped openings can be observed, one of which is sometimes in the middle, sometimes at the anterior edge of annulus 27, the other sometimes in the middle, sometimes at the anterior edge of annulus 31, and finally the 3rd in the furrow that divides annulus 31 from annulus 32. Annuli 27 and 31 are always noticeably wider and thickened on the ventral side. Probably 2 of the above named openings serve as openings for the genital organs, while the 3rd seems to be the outlet of some accessory gland of these organs". KOWALEVSKY (1896, No. 2) illustrated the position of these openings in *Acanthobdella* quite accurately: the 1st opening is separated from the 2nd by 3 annuli, while the 2nd is separated from the 3rd by 1 annulus. However, he did not interpret these openings correctly: he regarded the 2nd as an outlet of an accessory gland and the 3rd as the female genital opening. E. BRUMPT (1900, p. 349) wrote about this as follows: "Si nous regarderons maintenant l'animal par la face ventrale, nous apercevons en haut un premier orifice circulaire, c'est l'orifice mâle; un peu au dessous un second, transversal cette fois et assez irregulier, c'est 'orifice femelle, enfin au dessous un troisième découvert par GRUBE". This description and his illustration are certainly correct, but his following remark is a complete puzzle: "KOWALEVSKY dans son étude de l'*Acanthobdella*, signale également ce 3. orifice et le considèr comme celui de la glande placée en arrière du point de réunion des sacs ovariens". In KOWALEVSKY's illustration the latter opening is marked "female", and the former "g", meaning the outlet of the accessory genital gland, i.e. the exact opposite of the way in which BRUMPT interprets this illustration.

According to the author's own observations (Fig. 33, No. 1; Fig. 40, No. 93), the 1st (male) opening lies in the furrow between the 1st (9) and 2nd (10) clitellar somite; the 2nd female opening in the form of a lateral slit lies 3 annuli further, i.e. between the 3rd and 4th annulus of the 2nd clitellar somite (10). Another annulus further, i.e. between the 2nd (10) and 3rd (11) clitellar somite, is a slit-like depression (spt, Fig. 33, No. 1; Fig. 34, No. 9; Fig. 40, No. 93) which is also somehow related to the genital apparatus.

In the clitellar somites the nephridial openings are on the ventral intermediate line between the 1st and 2nd somite annulus, sometimes only in the 3rd somite (11); but sometimes it and the 2nd clitellar somite (10) have only indentations of the skin epithelium in the appropriate places, while these are usually absent, too, in the 1st somite (9); see Fig. 33, No. 1.

The clitellar region is followed by 8 somites (12-19) of the midgut region which are all equally well defined. They each have 4 well-developed annuli and 1 pair of nephridial openings in the furrow between the 1st and 2nd somite annuli which are situated as usual on the ventral intermediate line of the body. This can be very clearly seen in the illustration by KOWALEVSKY (1896, No. 7), although in his description he states that the nephridia "s'ouvrent à l'extérieur par des ouvertures placées sur les côtes du corps aux limites des somites", which is absolutely wrong.

Further caudad are 6 somites (20-25) of the hindgut region which no longer possess nephridial openings. The 2 most anterior of them (20, 21) each contain 4 well-developed annuli, i.e. they are typically formed as the somites of the midgut region. In the following 4 somites (22-25) a certain reduction can already be noted (Fig. 33, No.1; Fig. 35, No.16; Fig. 41, No.107). They usually consist of 3 annuli, since their last annulus has a lateral furrow only on the dorsal side; the furrow divides it here into two annuli, namely the 3rd and 4th of the ordinary somite, while such a furrow is completely absent ventrally. The anal opening (an) lies on the dorsal median line of the body in the furrow between the 4th (23) and 5th (24) somite of the hindgut region (Fig. 34, No. 13; Fig. 33, No. 1; Fig. 41, No. 108).

The body terminates in the attachment disk (26-29) which in contrast to the other Hirudinea is not in a horizonal but a vertical position, i.e. in continuation of the longitudinal axis of the body. Its diameter in my specimens was about 1.5 mm. From the outside 3 poorly defined annuli can be distinguished on the attachment disk (Fig. 33, No. 1; Fig. 35, No. 16; Fig. 41, No. 107). The most anterior annulus borders directly on the 6th somite (25) of the hindgut region, the most posterior annulus forms the posterior edge of the attachment disk. The concavity (hs) of the attachment disk which is turned caudad is not differentiated.

GRUBE (1851) wrote in this connection: "As far as the position of the very narrow anus is concerned, it is different than in Hirudinea in that it perforates the bottom of the posterior recessed disk somewhat below the middle ..." He continued: "The posterior end of the body is set off against the previous tract like a short cylinder and consists of 5 or more annuli, the last of which forms a somewhat deepened but certainly not widened disk with a bulging edge". KESSLER (1868) also stated that the attachment disk was poorly developed, "entirely pointing caudad and perforated in its centre by the anal opening, which does not occur in any other Hirudinea". KOWALEVSKY (1896, p. 269) already corrected these statements by GRUBE and KESSLER: "L'ouverture anale est placée sur la partie dorsal entre le 9. et 10. annaux en avant de la ventouse postèrieure ... La supposition de KESSLER que leur ventouse est peu développé et perforée par l'anus, est tout-à-fait inexacte, au contraire c'est un puissant organ d'attache".

When all these facts are considered together to determine the total number of trunk annuli of *Acanthobdella*, it is found that the number is 94 dorsally, while ventrally about 88 annuli can be distinguished. GRUBE counted only 80 annuli, but KESSLER, as cited above, quite correctly found the number of annuli to be 94.

Disregarding for the moment the other questions on the morphology of the "external" somite of *Acanthobdella*, we will now describe the internal organization of this worm.

The cuticulomuscular tube (body wall)

The body wall of *Acanthobdella* is a well-developed cuticulomuscular tube (Fig. 33, No. 2-6, Fig. 34, No. 7-14; Fig. 40, No. 96) which – as in the other Hirudinea – consists of the following components: the outer layer is the skin epithelium, followed by the musculature, and inside of it is the internal body mesenchyme which directly borders on the coelom.

2. The skin epithelium

The external body surface of *Acanthobdella* is covered with a layer of epithelial cells (ep); see Fig. 36, No. 23-30; Fig. 37, No. 47, 48, 51, 52; Fig. 38, No. 53; Fig. 40, No. 92. These cells secrete a colourless, thin cuticular membrane (cu), very easily separated by maceration from the epithelial cells that produce it; when separated, the membrane becomes structureless and is perforated by numerous small openings. The latter are outlets of the numerous glandular cells in the body wall.

The skin epithelium forms a single uninterrupted layer of cells whose behaviour, however, fluctuates greatly. In the middle sections of the somite annuli is a cylindrical epithelium (Fig. 36, No. 23-25, 27, 28; Fig. 37, No. 47, 48, 51, 52; Fig. 38, No. 53; Fig. 40, No. 92) whose cells have a more or less different appearance depending on the state of the worm. Sometimes the cells reach an average of 30-40 µ in length and a width of 4-5 µ, i.e. their shape is very elongated, but usually they are about 20 µ long and 8 µ wide. Since the cells are directly accumbent to each other, their contours in plane section are polygonal. Basally the epithelial cells lie on a mesenchymatous marginal layer (gl) which is often undulating in section (Fig. 36, No. 24-25) because the cells protrude more or less under the internal epithelial surface. This behaviour resembles relationships which are found to an even more developed degree in the other Hirudinea. This phenomenon is particularly obvious in specimens that have been fixed in osmic acid.

The otherwise finely granulated protoplasm of the epithelial cells is lengthwise fibrously striose in the distal sections of the cell body. The nucleus which is usually in the middle or basal sector of the cell, is of oval shape, about 8 µ long and 5 µ wide. It contains many fine chromatin grainlets; 1-2 relatively large nucleoli are always present. Sometimes typical mitoses are found in the described skin epithelial cells, and then the nuclear figures are always in the distal sector of the cell body.

In the annular furrows of the body (Fig. 36, No. 30), the elements of the skin epithelium are changed into flat cells of about 6 µ in length and a width of up to 14 µ. Their protoplasm always appears finely grained because it lacks distal striation. The nuclei are spherical in shape and have a diameter of 6-8 µ, but in their more detailed structure they do not differ from the above described nuclei.

Here and there among the ordinary epithelial cells, some very dissimilar elements can be observed (Fig. 36, No. 23 gep) which differ greatly from the adjacent cells (ep) in their large dimensions. They are of cylindrical or cubic shape and differ from the epithelial cells surrounding them in their width which can reach the height of the epithelium, but occasionally they are twice as wide as they are high. Their protoplasm is finely granulated; it stains quite deeply, and against the free surface a faint

(Please see p. 15a).

longitudinal striation can be seen.^Furthermore, a few rather large chromatin globules are present here.

Incidentally, the dimensions of the above described elements vary so much that the elements are occasionally almost as large as ordinary epithelial cells. However, they are always easily distinguished from the latter, and they definitely constitute a very special type of cell. No similar elements have been discovered in the other Hirudinea or in Oligochaeta. In passing it should be mentioned that the behaviour of these cells is similar to that of ciliated hoops found not only in larvae, but also in mature Spionidae and some other Polychaeta. However, no regularities in the distribution of these cells could be found in *Acanthobdella* It should only be mentioned that they usually do not occur ventrally.

The skin epithelium of *Acanthobdella* contains a large number of glandular and sensory cells as well as completely free elements which lie in the marginal layer and have probably migrated into the epithelium from the body mesenchyme. Furthermore, the rami of pigment-fat cells, the secretory ducts of glandular cells and the finest terminal rami (mf) of various muscle cells (Fig. 36, No. 24) all enter between the epithelial cells whose bodies lie under the epithelial layer, more or less deeply embedded in the mesenchyme. The delicate muscle fibres project between the epithelial cells as far as the cuticula, where they finally disappear; apparently they attach themselves to the cuticula.

The numerous glandular cells (dz) are present everywhere in the epithelium and are absent only in the furrows between the trunk annuli (Fig. 36, No. 27; Fig. 37, No. 47, 51, 52). Their shape and structure varies depending on their physiological state. In the initial stages of secretory activity the cells have about the same dimensions as the ordinary epithelial cells that surround them, except that their shape is different: they are basally broadened, while the distal section appears drawn out in the fashion of a collar. The broadened, basal section of the glandular cells protrudes somewhat under the lower epithelial surface, has a granulated protoplasm that is readily stained and contains a central or parietal nucleus which resembles the nuclei of the ordinary epithelial cells, from which it differs, however, in that it has coarser chromatin granules. During the further secretory process, the nucleus of the glandular cells always shifts into a completely parietal position, so that it is only covered by a very small mass

In accordance with the general dimensions of the cell body, the diameter of the round or oval corss-section of the nucleus is approx. 25-30 μ. The chromatin bodies in the nucleus are very delicate and not very numerous.

of protoplasm. The basal cell section begins to fill with secretion, while the cell itself becomes enlarged and tubular. Next, the elimination of the secretion takes place, after which the cell walls collapse until only a small transparent cell can be seen that contains in its base a small protoplasm rest. The nucleus contained in the latter becomes heavily stained throughout, and its detailed structure cannot be observed.

On the one hand, the above glandular cells resemble quite strongly the hypodermal glands of the Glossosiphonids described by E. BAYER (1898). One difference is that in the latter case they penetrate even deeper into the body mesenchyme. On the other hand, they are also very similar to the mucous glands in the skin of many Oligochaeta.

Furthermore, in *Acanthobdella* special unicellular skin glands occur whose cell bodies are completely embedded in the body mesenchyme; they will be discussed together with the latter.

Another category of elements also occuring between the ordinary epithelial cells is formed by the sensory cells.

3. The sensory cells

The sensory cells are organized as sensory organs, either individually or in groups.

The different sensory cells are distributed throughout the epithelium without any discernable regularity. They are spindle-shaped and of the same hight as the adjacent elements. Their protoplasm is quite readily stained. Their nucleus is of similar appearance as that of the other epithelial cells, but it has slightly more chromatin granules. In the cell section where the nucleus is situated, the protoplasm forms a minor thickening. The basal section of the sensory cells terminates in a fine, long process which enters one of the nerve bundles of the body wall.

The above described sensory cells merge into more or less significant groups, forming the simplest kind of sensory organs, so-called sensory buds (Fig. 36, No. 25 sk). In exactly the same way as in the other Hirudinea, these sensory buds project as oval or club-like masses under the general lower surface of the dermal epithelium where they lie between the annular and diagonal muscles. Their outermost cells often extend as far as into the longitudinal musculature.

The majority of these elements forming the sensory buds consist of well-developed sensory cells. Their oval or round nuclei, about 7 µ in diameter, lie in the cells at a greatly varying height. In the midst of these elements, basally in many sensory buds are 1-3 cells of a special type (rz). They are considerably larger than the sensory cells that surround them, have an irregular, polygonal shape and a basal process that enters the sensitive nerves. Their protoplasm is finely granulated and stains very deeply. The nucleus has an oval or round shape in section and reaches up to 12-15 µ in diameter. It contains many very delicate chromatin granules and a few coarser chromatin globules. In this cell section, distad from the nucleus, a type of vacuole can be observed whose dimensions fluctuate very considerably. The larger vacuoles, generally of oval shape, measure about 10-12 µ in diameter. When they are completely developed, a peripheral, finely radially striated layer can be recognized. Such cells of the sensory buds can already be regarded as so-called retinal cells or, as suggested by S. APATHY (1901), as subepidermal sensory cells, the equivalent of the corresponding elements in the other Hirudinea and Oligochaeta.

The fact should be mentioned that the above described subepithelial cells of *Acanthobdella* are very similar to the ganglial cells which will be discussed below and with which they can easily be mistaken when the light-refracting internal body is poorly developed or absent. S. APATHY (1901) mentioned the same phenomenon in the other Hirudinea, as R. HESSE (1896) did in Lumbricidae. The author did not observe any subepithelial cells unconnected with sensory buds in *Acanthobdella*, and it appears that this is the rule in Hirudinea, notwithstanding statements by authors who claim the opposite. However, it is possible that the retinal cells are at a certain distance from their sensory bud which leads to the impression that these cells are quite independent; but this would surely have to be interpreted as a secondary phenomenon.

The sensory buds (sk) do not seem to be evenly distributed in the somite of *Acanthobdella* (Fig. 40, No. 97). They are almost completely absent in the 4th and 3rd somite annulus, and the dorsal sector of the 1st somite annulus contains only a small number of rather poorly developed buds. On the other hand, the sensory buds are well-developed and regularly distributed in the 2nd annulus of the somite, which – similar to the middle annulus of the somite in the other Hirudinea which corresponds to the middle sector of the somite in Oligochaeta – can be regarded as the exquisitely sensitive somite annulus. Also connected with this is the fact that – as will be seen below – the only sensitive nerve (sn) of the somite of *Acanthobdella* lies in the 2nd somite annulus.

Only rarely can very isolated sensory buds be observed. In most cases, two or three are found closely together, but sometimes groups of four sensory buds occur. In the ventral sector of the 2nd somite annulus, two groups of sensory buds are usually found, namely one closer to the median line of the body, the other closer to the lateral line (Fig. 34, No. 8). The same is found in the dorsal sector of this annulus. On the lateral line is another rather important group of sensory buds. A comparison between the distribution of the sensory buds and their very regular arrangement in the middle somite annulus of the other Hirudinea along certain longitudinal lines of the body, shows the following: while in the other Hirudinea a lateral section of a body line corresponds to only a single sensory bud or sensillum, several such sense organs are grouped together along the same body line in *Acanthobdella* This is easily explained when the groups of 2-3 sensory buds which occur toward the median dorsally as well as ventrally in the 2nd somite annulus, are regarded as corresponding to the sensory buds which in the other Hirudinea lie at the two paramedian lines of the body (pmd, pmd_1). The other groups of these organs which occur laterally in the 2nd somite annulus, correspond to the sensory buds in the other Hirudinea which are distributed laterally of the paramedian lines, and among those in particular the intermediate line, for which reason the body line in question (int, int_1) in *Acanthobdella* can apparently be compared with the intermediate line in the other Hirudinea. The larger group of sensory buds at the lateral line, where these organs are usually poorly developed in the other Hirudinea, would finally correspond to both the dorsal and ventral paramarginal sensory buds in the latter. Occasionally in *Acanthobdella* the lateral sensory buds have shifted ventrally or dorsally, i.e. they are arranged along the paramarginal lines of the body. A certain irregularity in the distribution of the sensory buds is manifested by the fact that some are occasionally somewhat remote from the corresponding groups, or that one and the same group may contain a different number of sensory buds in different somites.

In our further discussion we will see that the musculature and the nervous system of *Acanthobdella* allows the distinction of these same body lines which have been determined here on the basis of the distribution of the sensory organs.

At the end of this description it should be noted that all sensory buds of a somite are more or less equally developed. A differentiation of the kind that is found in the sensilla and sensory buds of the other Hirudinea, does not occur in *Acanthobdella*, although some sensory buds at the lateral line of the body usually show a more significant degree of development, and contain well-developed subepithelial cells, similar to the typical sensilla of the other Hirudinea.

The eyes of *Acanthobdella*, which occur only in some head somites, will be discussed in detail together with the head region.

4. The musculature

The literature contains descriptions by two authors on the musculature of the body wall in *Acanthobdella*. E. GRUBE (1851) wrote: "The structure of the body wall shows muscle fibres running in various directions, but predominantly longitudinal fibres". A. KOWALEVSKY (1896. p. 267) wrote: "L'*Acanthobdella* comme la plupart des Annelides possède une ligne latérale qui est assez nettement visible sur les individus traités au sublimé et conservés dans l'alcohol. Ces individus, comme nous l'avons déjà dit, perdent leur pigment, et on aperçoit alors très distinctement sur les parties latérales de leur corps, à la limite de leurs somites 20 ou 21 taches blanches, indiquant les lignes latérales. Chacune de ces taches blanches est formée d'une très grande cellule musculaire, posée immédiatement sous les tegument et dont les prolongements donnent des fibres circulaires – muscles sirculaires" ... (p. 268) "Il ne faudrait pas penser, que tous les muscles circulaires sont formés par les prolongements de cellules musculaires de la ligne latérale, il y a des muscles circulaires qui sont formés par des petites cellules du même type nématoïde, et des simples cellules musculaires, c'est à dire des cellules dont la périphérie est formée par la substance contractile et l'intérieur par le protoplasma contenant le noyau".

This very sparse information was all that had thus far been known about the musculature of the body wall of this worm.

In the cuticulomuscular tube of *Acanthobdella*, 3 muscle layers can be distinguished, all very clearly differentiated from each other (Fig. 33, No. 3-6; Fig. 34, No. 7-13; Fig. 36, No. 26-30; Fig. 37, No. 49-52; Fig. 38, No. 53; Fig. 39, No. 82; Fig. 40, No. 92, 96). Directly below the skin epithelium lies a layer of annular fibres (rm), followed by the diagonal muscle layer (dm), from which the longitudinal muscles (lm) run mediad. Thus in general, the muscles of *Acanthobdella* are of a very characteristic Hirudinea type. In contrast, the Oligochaeta usually have only 2 layers: an outer annular layer and an inner layer of longitudinal muscles. According to F. SCHMIDT (1903), only *Branchiobdella* has characteristics similar to the Hirudinea. M. DE BOCK (1901) also found the diagonal musculature in *Lumbriculus* and some Naidomorpha, and the author can certainly confirm his findings. However, this does not change things, since the diagonal muscles in the above named forms lie directly below the skin epithelium, i.e. outside the annular musculature, while in Hirudinea and *Branchiobdella* they are always embedded between the annular and longitudinal muscles.

We will first deal with the annular muscle layer (rm) of *Acanthobdella*.

The individual cells of the circular muscles (rm) are spindle-shaped (Fig. 35, No. 20; Fig. 36, No. 26-29; Fig. 37, No. 49). The periphery which is round or oval in section consists of the contractile substance, while the axis is filled by the cell's unchanged protoplasm. In the contractile layer, a fibrillar structure can be observed that is the same as in the other Hirudinea. The protoplasm can be readily stained, is finely granulated and of a coarsely-meshed structure, with the mesh arranged radially to the periphery. Approximately in the centre of the cell, where the protoplasm has no mesh and is very dense, lies the nucleus which is of oval shape, elongated in the direction of the fibre, and containing many small chromatin granules, a few chromatin globules, and one or two nucleoli. In the section of the muscle cell that contains the nucleus, the contractile-fibrillar peripheral layer is always absent over a varying length of section. Very rarely cells can be observed (Fig. 36, No. 28) where only a small slit is present in this layer; in such cases, the plasm does not project outward, and the cell therefore retains smooth contours throughout. However, the author never found cells structured strictly according to the Hirudinea type, and A. KOWALEVSKY's statement about the presence of "simple cellules musculaires" would therefore have to be disputed. They must have been the above described cells which he mistook for typical Hirudinea muscles cells.

A type of annular muscle elements of *Acanthobdella* are the cells (Fig. 36, No. 27, 29) in which the contractile-fibrillar layer is absent along approximately half the periphery of the nucleate cell section, and where the latter – in the fashion of an oval muscle body – is mounted on the inside of the contractile-fibrillar layer that faces distally (i.e. toward the epithelium). A. KOWALEVSKY (1896) called such cells "nématoïde"; they are very similar to those described by the author in the annular and dorsoventral muscles of *Hemiclepsis marginata* (LIVANOW, 1902, 1903).

A rare occurrence in *Acanthobdella* are annular muscles (Fig. 36, No. 26) whose nucleate section is pear-shaped and protrudes between the longitudinal muscles. The oval nucleus in such cells is transversely striated in relation to the muscle fibre.

The above mentioned facts indicate that the structure of the annular muscle cells of *Acanthobdella* differs only insignificantly from that known as typical in Hirudinea, while it differs far more from that of Oligochaeta. Among Oligochaeta, the "simple spindle cells" described by F. SCHMIDT (1903) in the annular musculature of *Branchiobdella* are similar to those in *Acanthobdella*. The only difference between these and the muscle cells of *Branchiobdella* is the degree of development of the contractile-fibrillar substance which is less developed in *Acanthobdella* and the other Hirudinea. As we will see, this is also true of the longitudinal muscle fibres of both species and is therefore a general rule. The "double muscle cells" of *Branchiobdella* on the other hand do not occur in *Acanthobdella*, while they seem to be characteristic for many Oligochaeta.

In reference to the position of the nucleate cell section of the annular muscles of *Acanthobdella*, it should be noted (Fig. 35, No. 20) that it is usually near the lateral line of the body (l). More rarely one encounters cells in which this section has shifted more or less toward the median, approximately to the outer paramedian line. Thus the median field of the body always remains without them, dorsally as well as ventrally. This characteristic forms an intermediate step between the irregular position of the nuclei in the majority of Hirudinea on the one hand and their arrangement in *Branchiobdella* on the other. In the latter form, E SCHMIDT (1903, p. 610) differentiated 3 "rows of annular muscle nuclei" on each side, namely a "dorsal, ventral and lateral" row, corresponding to the lateral and intermediate as well as the ventral and dorsal lines of the body. However, it should be noted here that such a regular distribution of the nuclei in *Branchiobdella* seems unlikely. It is more probable that the nuclei are simply more or less grouped near the lateral line, and that their position therefore only approximates the very regular arrangement of the lateral line in most Oligochaeta.

Acanthobdella also provides us with interesting facts in reference to the varying behaviour of the nucleate section of the annular muscle cells. Not only can the structural situation resemble typical Hirudinea muscles, we are also reminded of the Oligochaeta type, and in *Acanthobdella* too, the nucleate section can intrude between the longitudinal muscles similar to the annular muscle bodies in the lateral line of Oligochaeta, as described by R. HESSE (1894) and others.

Each somite annulus of *Acanthobdella* (Fig. 35, No. 20) contains approximately 8-10 circular muscle cells, so that the entire annulus contains about 20 cells. They are arranged in the annulus in a layer, forming a very regular bundle of circular muscle fibres. Below each annular furrow between the two adjacent annuli, is a muscle cell whose nucleus lies in a strictly lateral position. It traverses about 3/4 of the body periphery, and only over about 1/4 of the way, namely at the lateral line, it runs alone, while further ventrally and dorsally it is joined by the corresponding fibre from the other side, so that both together form a full muscle ring. Fore and aft, each such cell is usually accompanied by a similar, but somewhat less developed muscle cell. Between these circular muscle bundles (mf) which make up the edges of the annuli, the annulus contains usually 4 bundles of circular muscle fibres. However, these contain usually (a) only one muscle fibre on each side whose relationships are similar to those just described, or (b) 4 muscle cells participate in the composition of the circular muscle bundle, two on each side, in which case the nuclei of the cells are situated at the lateral and intermediate line of the body, and the fibrous processes are unevenly long. While the process toward the lateral line ends near that line, the other runs as described in connection with the above muscle fibres, i.e. it is much longer. Such muscle bundles are usually observed forward of the annular furrow in the posterior section of each annulus. However, bundles of both types may alternate without any regularity.

A similar arrangement of annular muscles in bundles has been described in Oligochaeta, especially by F. SCHMIDT (1903) in *Branchiobdella*

According to A. KOWALEVSKY (1896, p. 267), some of the annular muscle fibres are formed by projections of the "cellules musculaires de la ligne laterale". This is incorrect, since the described cells form the origin of others, namely those of the diagonal muscle layer (dm). This layer is so well-developed (Fig. 36, No. 26-29; Fig. 37, No. 49-52; Fig. 40, No. 92) that they can be very easily recognized if the section has been made in the right direction.

Between the 1st and 2nd annulus of each somite, a colossal muscle cell is situated on each side of the lateral line (l) of the body (Fig. 33, No. 6; Fig. 34, No. 12; Fig. 35, No. 21; Fig. 36, No. 29, 30 dm*). The processes (mf) of these 2 cells form the entire diagonal musculature of the somite in question (Fig. 35, No. 21). The cell itself is of spherical or oval shape and reaches a diameter of approximately up to 140 μ. Its protoplasm is finely granulated and can be readily stained. The nucleus has a diameter of about 90 μ and contains a large amount of chromatin granules and globules, and a large nucleolus. These cells project into the inner body mesenchyme at the lateral line of the body between the longitudinal muscles.

The processes run in two directions from the cell body surface that is directed toward the epithelium: those forming the posterior section of the cell run ventrad and caudad, the others from the anterior part of the cell dorsad and cephalad, i.e. into the 1st annulus of the somite and further. All these extensions are surrounded by the fibrillar-contractile layer even at their origin, and this layer continues on the cell body itself in the form of more or less wide lamellae, usually broadening on the lateral surface of the cell (i.e. toward the epithelium). In the vicinity of the cell body, the fibres divide into their branches which then continue unchanged. However, some of the diagonal muscle fibres do not come directly from the cell body, but from a protosplasmic process which as usual lies between the circular and longitudinal muscles. The upper section of the cell body expands dorsad and caudad, i.e. into the 2nd annulus of the somite, and from this process of the same, diagonal muscle fibres usually run in the two above named directions. The length of this process is not great, and it does not reach as far as the paramarginal dorsal line.

The diagonal muscle fibres of a somite thus originating in two cells form only a single layer dorsally and ventrally, but laterally two clearly differentiated layers can be observed, because this is where the cell lies with its fibres toward the inside in relation to the processes of the cell on the other side. Thus at the median lines is the point where the fibres cross and change their position: the fibres first running on the inside now continue outside of the fibres running in the opposite direction. The diagonal muscle fibres of one side cross those of the other side at an angle of about 60° and 120°, respectively.

Although, as we have seen, a layer of diagonal muscle fibres as in the other Hirudinea occurs in *Acanthobdella*, it is formed in a significantly different manner. It practically represents an intermediate stage between the Hirudinea on the one hand, and *Branchiobdella* on the other. According to F. SCHMIDT (1903), the diagonal musculature in the latter is formed at each side of each somite by only 2 cells. Similarly as in *Acanthobdella*, the nucleate sections of these cells are at the lateral line of the body, but each forms only 1 or 2 muscle fibres; that is why the entire diagonal musculature is very poorly developed in that area. In the Hirudinea, on the other hand, very numerous muscle fibres are present on both sides, and each fibre always constitutes an independent muscle cell. As the author was able to determine in *Hemiclepsis marginata* and *Piscicola piscium*, the nucleate cell sections are sometimes also quite regularly distributed at the ventral paramedian line of the body. Another important difference occurs in *Branchiobdella*: the direction of the diagonal muscle fibres is exactly opposite to that in *Acanthobdella* and the other Hirudinea. In leeches, the fibres run dorsally cephalad and ventrally caudad from the nucleate cell section. In *Branchiobdella* they run dorsally caudad and ventrally cephalad, and in this respect the author can fully confirm the findings of F. SCHMIDT (1903).

This behaviour seems to be an indication that the development of the diagonal musculature in *Branchiobdella* and *Acanthobdella* could have had a common source only in its first origin, while the different forms must have followed a different direction later.

In comparison with the other Hirudinea, the longitudinal musculature of *Acanthobdella* is not well-developed. Only poorly defined longitudinal muscle strands composed of a small number of muscle fibres are found (Fig.

33, No. 2-6; Fig. 34, No. 7, 13; Fig. 35, No. 22; Fig. 36, No. 28, 31; Fig. 37, No. 45, 47, 49; Fig. 39, No. 82; Fig. 40, No. 96).

Distally, i.e. toward the epithelium, the latter contain muscle fibres whose structure is similar to that of the above described annular muscle fibres (Fig. 36, No. 26-31; Fig. 37, No. 45-52; Fig. 38, No. 53, 59; Fig. 39, No. 82; Fig. 40, No. 92). They are spindle-shaped, only rarely slightly ramified at the ends; they measure about 10-20 µ in round or oval section. On the periphery is a contractile-fibrillar layer, and inside is the unchanged protoplasm. The cell section containing the oval nucleus now shows a large number of variations. There are fibres in which this nucleate section is a pear-shaped protrusion, and where the contractile-fibrillar layer is only a narrow plate that is outwardly (i.e. toward the epithelium) adjacent to the plasma (Fig. 38, No. 53 lm*). This is followed by the most common behaviour (Fig. 36, No. 31; Fig. 38, No. 59) where the contractile-fibrillar layer is U-shaped in section, and where the space between the two legs of the U is filled with plasm. A transition toward the actual Hirudinea type is formed by the muscle fibres (Fig. 37, No. 47, 49-51) in which the contractile-fibrillar layer expands across the major portion of the nucleate section, leaving only a narrow slit open toward the middle.

Finally in the longitudinal muscle bundles we find fibres (lm_1) which are formed as those typical for Hirudinea in that their contractile-fibrillar layer is uninterrupted along the entire periphery of the cell (Fig. 36, No. 27; Fig. 37, No. 45; Fig. 39, No. 82). Such fibres are situated at the far proximate end, toward the mesenchyme, while they are usually completely absent distally. They represent the largest muscle elements of the longitudinal musculature and reach up to 40 µ in diameter.

While all structural details of these latter fibres are typical for Hirudinea, the above described longitudinal muscle fibres have characteristics which are identical to those in longitudual muscle strand cells described by the author (1903) and which also resemble the structure of annular and dorsoventral muscle cells of *Hemiclepsis.* Among Oligochaeta, similarly structured longitudinal muscle cells occur in *Branchiobdella.* In the author's opinion, these are of the same type as those in *Acanthobdella*, but are somewhat strangely formed, particularly as far as their powerful development of the contractile-fibrillar substance is concerned. Another link in the same line of development is *Haplotaxis*, where the fibrillar layer is of an irregular V-shaped section. While the entire longitudinal musculature of this form resembles the characteristics described in *Branchiobdella* and *Acanthobdella*, M. BOCK (1901) points out that similar characteristics can be found in other Oligochaeta, such as *Lumbricilus* and the Lumbricidae, only in some of the most distal longitudinal muscle fibres.

However, *Acanthobdella* additionally has longitudinal muscle fibres which are formed as is typical in Oligochaeta (Fig. 36, No. 28). There are 2 fibres (olm) on each side which lie proximally between the regular longitudinal muscles (toward the coelom) inside the strands and run in the area of the ventral paramedian line (pmd_1) and the dorsal paramedian line (pmr) of the body (Fig. 33, No. 3-6; Fig. 34, No. 7-13; Fig. 35, No. 22; Fig. 40, No. 96). These fibres are very thin and poorly developed in comparison with the muscles that surround them. Their contractile-fibrillar substance is forming a plate standing on edge on which a small remnant of protoplasm is mounted, but the latter is present only in the vicinity of the somite limits, while it is absent over the greater extent of the fibre. In the extension of this plasm remnant is the nucleus of the muscle cell which lies either in annulus 1 of the somite or somewhat more cephalad or caudad of the latter, respectively. The individual cells in these longitudinal muscle fibres adhere so closely to each other that one might think they extended over the entire length of the body, but their nucleate cell sections clearly indicate that they are composed of several, linearly successive cells. The individual muscle cells in the head region are indeed distinctly delineated from each other, and they do not lie as closely here as in the middle part of the body. Each cell is a little longer than the corresponding somite.

This investigation of the histological structure of the longitudinal musculature of *Acanthobdella* shows that some of the muscle cells have been formed according to the Oligochaeta type, others according to the Hirudinea type. However, by and large the general character of the longitudinal musculature certainly resembles that of Hirudinea, although these muscles are less differentiated in comparison to the latter. They therefore represent a lower degree of development, forming a transitional stage between the musculature of Oligochaeta and that of Hirudinea.

These facts lead to certain conclusions. The muscle cells of Oligochaeta as well as those of Hirudinea probably originated in muscle cells which in a part of their periphery, especially distally, had developed the contractile-fibrillary layer and whose nucleate section formed a more or less developed proliferation of protoplasm. This original form could be derived almost directly from the epithelial muscle cell. In the further course of development, either the contractile-fibrillar layer in the cell differentiated over the major portion of the periphery, resulting in the Hirudinea muscle cell, or the contractile-fibrillar layer assumed the shape of a plate when both legs of the fibrillar layer (which is V-shaped in section) came to adhere closely together, thus displacing the plasm and the nucleus distally and resulting in the typical Oligochaeta muscle cells. In this case, the author is in full agreement with views already expressed by R. HESSE (1894).

As mentioned, the longitudinal muscles of *Acanthobdella* form more or less well-developed longitudinal muscle strands, although their proportions are never as large as they always are in Hirudinea. On the other hand, the longitudinal muscle cells in the middle body sector (Fig. 34, No. 10; Fig. 40, No. 96) are commensurate to that sector's larger dimensions and arranged in a single layer: almost the same number of muscle cells are distributed here over a much larger area.

However, some longitudinal muscle strands occur as very definite, always present groups of fibres (Fig. 35, No. 22; Fig. 33, No. 2-6; Fig. 34, No. 7-13; Fig. 40, No. 96). To these belong the strands situated on the lateral line (lb), ventrally and dorsally on the paramedian line (pmd_1, pmd), on the intermediate line (int_1, int) and the paramarginal line (pmr_1, pmr). As we will see, these are very closely related to the motor ring nerves of the somite, while the other longitudinal muscle strands do not have such relationships. The former strands are the only ones remaining in the 2 anterior head somites (Fig. 38, No. 61) because the other longitudinal muscles terminate earlier. These facts, which will be discussed further, lead to the assumption that the 2 lateral, 6 dorsal and 6 ventral longitudinal muscle strands might have formed the basis on which the entire longitudinal musculature of the body was built.

Independently of the muscle layers just discussed, *Acanthobdella* possesses a musculature that traverses the body in dorsoventral and diagonal direction (Fig. 33, No. 5, 6; Fig. 34, No. 10, 11). Among the former are those muscles (dvm) which attach themselves to the body integument with their terminal processes dorsally near the paramedian line, ventrally toward the median. The diagonal muscle cells (sm) attach themselves dorsally near or laterally of the paramarginal line, ventrally at the intermediate line of the body. Both types traverse the inner body mesenchyme (ms), and most of their length is found there.

They are ordinary muscle cells of medium size whose ends are slightly ramified. Their nucleate section is without a fibrillar-contractile layer over a varying length of the periphery, and the plasm often forms a kind of muscle particle here in whose centre the nucleus is situated.

The diagonal muscle cells are arranged quite regularly: on each side about one occurs in each annulus of the somite (Fig. 33, No .5, 6; Fig. 34, No. 10), where their position, however, seems to be more or less uncertain. Sometimes they are situated in the annulus itself, sometimes almost or completely in the furrow between two adjacent annuli. As they traverse the inner body mesenchyme, the diagonal muscles usually lean directly against the lateroventral longitudinal muscle strands. In the preclitellar somites and in the posterior somites of the middle body, on the other heand, these cells are somewhat distant from the longitudinal muscles and protrude more into the mesenchyme; in the somites containing testes they sometimes even curve proximally around the former, i.e. they run very close to the central coelom.

The dorsoventral muscle cells (dvm) are in the preclitellar somites where one occurs quite regularly on each side of each annulus, directly leaning against the lateral coelom wall in the inner body mesenchyme (Fig. 33, No. 5). The muscle cells of the 4th annulus usually already belong to the dissepiment. However, in the somites containing testes, all dorsoventral muscle cells seem to be concentrated in the dissepiment. As a rule 2 (Fig. 34, No. 11) or 3 (Fig. 37, No. 39) cells occur in the dissepiment lamella itself, and one other cell runs directly cephalad or caudad of the latter.

As far as this behaviour of the dorsoventral and diagonal muscles is concerned, *Acanthobdella* is a transitional form between the Oligochaeta – where these muscles are mostly embedded in the dissepiment itself – and the other Hirudinea – where they are scattered throughout the entire inner body mesenchyme.

In the hindgut and attachment disk region of *Acanthobdella*, the dorsoventral and diagonal muscles have undergone considerable changes in position and, albeit to a lesser degree, in structure. Here the diagonal muscles are no longer regularly arranged, and their attachment points deviate quite sharply from the ordinary behaviour. As far as their structure is concerned, a greater number of more less well-developed rami can be found. The dorsoventral muscles (Fig. 36, No. 32), almost all of which are embedded in groups of 3-4 in the dissepiment lamellae of the deep constrictions of the hindgut, show the same peculiarities. Their contractile-fibrillar layer has very many smaller or larger rami along the entire length of the cell. Therefore the nucleate section contains this layer in the form of several plates distributed on its surface, between which the protoplasm is exposed. In terms of their structure, these cells very much resemble the dorsoventral dissepiment muscles of *Branchiobdella*. By means of transitional forms they are very closely related to the ordinary dorsoventral muscle cells of the middle body section, where these already have a very similar structure as the dorsoventral muscles of *Hemiclepsis*.

The musculature of the head of *Acanthobdella* will be discussed in connection with a general description of the head region.

5. The mesenchyme

Under the skin epithelium all spaces between muscle fibres are filled with mesenchyme, which is particularly thick under the longitudinal musculature, causing a strong reaction in the coelom of *Acanthobdella* (Fig. 33, No. 2-6; Fig. 34, No. 7-13; Fig. 40, No. 96). In contrast to the Oligochaeta, this behaviour is particularly characteristic for the Hirudinea. As is customary in the latter, the author defines the inner body mesenchyme (ms) as the mesenchyme layer situated proximally of the longitudinal muscles, between the latter and the coelom wall.

A. KOWALEVSKY (1896, p. 267) described the situation as follows: "Tous ces éléments qui composent les parois du corps sont entourés d'un tissu conjonctif muqueux, plus ou moins fibrilleux dans des différents endroits, qui contient encore un petit nombre de toutes petites cellules ... Ainsi dans les parois du corps nous trouvons non seulement la couche proprement dermique, mais aussi un développement considérable du tissu conjonctif dans lequel sont placés les muscles, les cellules pigmento-adipeuses, les cellules glandulaires, et les glandes génitales mâles, ce qui présente certaine ressemblance avec de vrais Hirudinées oú le parenchyme du corps est si développée".

The body mesenchyme (ms) of *Acanthobdella* is formed by a glassy, colourless mass of jelly (Fig. 36, No. 26-28, 30; Fig. 37, No. 41, 52; Fig. 38, No. 53, 58, 59; Fig. 39, No. 82; Fig. 40, No. 92) that has no structure; in spite of several different methods used, it stains only faintly if at all. For example, when stained with hematoxylin/acid fuchsine/picric acid (after VAN GIESON), it turns only a pale pink.

However, below the skin epithelium, around the nerves and muscle cells, and below the coelothelial lining of the coelomic sinuses, the mesenchyme forms fine marginal layers (gl) that can be stained very readily with the same dyes which elsewhere produce a hardly discernable coloration of the mesenchyme. For example, when the above named staining method after VAN GIESON is used, these marginal layers absorb the very deep colour of acid fuchsine. Connections between the individual marginal layers are generally not often observed, but it happens not too rarely that one sees that they are interconnected by means of ragged membranes or fibres which have the same characteristics as the marginal layers (Fig. 36, No. 32; Fig. 37, No. 47, 51, 52; Fig. 38, No. 53).

The author was unable to confirm that the mesenchyme of *Acanthobdilla* is of fibrillar structure, as A. KOWALEVSKY (1896, l. c) claimed. In this respect, the mesenchyme of this worm is made of a more primitive, less differentiated tissue than the mesenchyme of the other Hirudinea. In the Rhynchobdellidae, the mesenchyme always contains albeit still relatively poorly developed fibrillar structures which can be stained more deeply with VAN GIESON's acid fuchsine method than the jelly-like mesenchyme mass of *Acanthobdella* In the Gnathobdellidae, on the other hand, this tissue forms a well-developed network of sharply differentiated fibrillae which can be deeply stained with acid fuchsine. In all these cases, we can see that the fibrillar structure of the mesenchyme does not result from the development of fibrillar formations at the expense of mesenchyme cells, but represents only the differentiation product of a structureless basic substance. Thus the mesenchyme of Hirudinea should be regarded as a specific tissue that is generally characteristic for the latter and has only different degrees of differentiation in the various groups of Hirudinea.

In the mesenchyme of *Acanthobdella*, small, freely mobile cells (am) are scattered here and there, albeit in considerable number (Fig. 36; No. 26-30, 35; Fig. 37, No. 46-52; Fig. 38, No. 53, 58; Fig. 39, No. 82; Fig. 40, No. 92). There are of very variable shape, the majority being oval or spherical, reaching a diameter of up to 10 μ. Occasionally one sees cells whose spindle shape and more delicate structure resembles the mesenchyme cells of the other Hirudinea, especially the Gnathobdellidae. Their finely granulated protoplasm is fairly faint when stained; the oval or spherical nucleus reaches up to about 6 μ in diameter and contains an insignificant number of small chromatin granules and 2-3 coarser chromatin globules. As we will see below, these elements are identical with the free coelomocytes and haemocytes. They are nothing but free amoebocytes of the mesenchyme. Genetic relationships seem to exist between them and the coelomocytes, and it often seems that the coelomocytes break through the coelom wall into the body mesenchyme. However, lacking observations with live specimens, the author is unable to state this with certainty.

In addition to the amoebocytes, the mesenchyme also contains peculiar free cells (pz: Fig. 36, No. 26, 27, 29, 33, 34; Fig. 37, No. 48; Fig. 38, No. 53; Fig. 40, No. 92) which occur exclusively between or on the muscle fibres of the body wall. A KOWALEVSKY (1896) described these elements in great detail (p. 266): "La coloration [of the body] dépend des grandes cellules pigmentées disposées dans les parois du corps, principalement sous les muscles longitudinaux oú elles forment une couche prèsque continue. Ces cellules sont très grandes, le pigment ... est disposé à la périphérie de la cellule, tandis que l'intérieur de la cellule est rempli de granules adipeux ..., entourant le grand noyan de la cellule ... Ces cellules donnent des nombreuses ramifications pigmentées, qu pénétrent entre les fibres musculaires, les entourent et se prolongent dans la couche cutanée, jusqu'aux cellules épithéliales et même pénétrent parmi ces dernières. Quelques fois on voit que les cellules pigmentées, ainsi non seulement les ramifications des cellules pénétrent au dessus des muscles longitudinaux et se disposent immédiatement sous l'épithélium extérieur du corps. Ces cellules sont comme nous l'avons déjà dit en même temps pigmentaires et adipeuses, leur partie extérieure contient de très petites granules pigmentaires, tandisque l'intérieure est occupé par des granules adipeux beaucoup plus grands. Leur pigment se dissout dans l'alcool et on ne voit alors que les grandes cellules parenchymateuses, remplies de granules adipeux. Si on traite l'*Acanthobdella* par l'acide osmique, ou le liquide de HERMANN, on réussit à conserver le pigment, et alors sur les coupes colorées par example par la safranine, on voit au centre de la cellule le grand noyan coloré en rouge, puis les granules adipeux, colorés en noir par l'acide osmique et les grandes pigmentaires bruns, occupant la périphérie".

The author has to add little to this description by A. KOWALEVSKY (1896). The protoplasm of the described cells is finely granulated and stains quite deeply. The nucleus, which reaches up to about 30 μ in diameter, is of spherical shape, contains many fine chromatin granules and 5-6 larger chromatin globules. Occasionally one notices cells which have 2 quite identical nuclei, but the author was never able to detect mitoses in these cells.

The pigment-fat cells appear to be mesenchyme elements characteristic for *Acanthobdella* The other Hirudinea do have cells which are certainly closely related to those decribed, but they represent a further degree of differentiation; they are on the one hand the actual pigment cells, which contain only pigment granules, and on the other hand elements containing only fat and other fatlike reserve substances. A. GRAF (1899, p. 338) assumed that closer relationships existed between these two types of cells in Hirudinea. This can be confirmed because *Acanthobdella* has only one type of cell which serves as pigment and fat cell at the same time, while other elements containing pigment granules or fat inclusions are absent in the mesenchyme.

In addition to the described elements, the mesenchyme also contains gland cells. They include two clearly differentiated cell types, although both prove to be derivates of the skin epithelium.

One type consist of small gland elements (adz: Fig. 36, No. 28, 34) which usually lie in the mesenchymatous spaces between the longitudinal muscles of the body. The spherical or oval cell body of these glands, about 10 μ in diameter, continues imperceptably into the secretory duct whose diameter is only a little smaller than that of the cell itself. The distal sector of the secretory duct traverses through the skin epithelium cells and narrows only just below the cuticula, in the immediate vicinity of the glandular opening. The protoplasm of these cells remains only in the proximal part of the cell body in the form of a few stainable strands. The nucleus is centrally situated and can only be differentiated from the nuclei of the ordinary skin epithelium by its coarser chromatin granules. These gland elements whose secretory ducts seem to be distributed over the entire body surface, albeit in insignificant number, certainly resemble the albumin glands of the Hirudinea and Oligochaeta.

The second type of skin glands (gdz) is characterized in that here the cell bodies lie exclusively in the inner body mesenchyme (Fig. 33, No. 4-6; Fig. 34, No. 7-12; Fig. 36, No. 35; Fig. 40, No. 96). A. KOWALEVSKY (1896, p. 266) wrote about these elements: "Nous trouvons dans les parois du corps des cellules deux ou trois fois plus grandes que les cellules pigmentaires; ce sont de vraies cellules géantes ... Elles sont pyriformes, et leur bout pointu se prolonge dans des canaux excréteurs, propres à un group de ces cellules".

In the inner body mesenchyme of *Acanthobdella* we find clusters of glandular secretory ducts (aup) quite equally distributed below the longitudinal musculature. In the middle portion of the body, beginning at about the 3rd somite (14) of the midgut region, these clusters uninterruptedly run cephalad into the head end, and caudad into the attachment disk region. The clusters running in the latter direction gradually increase in size and open outwardly, also regularly distributed over the concavity of the attachment disk, without showing any special kind of grouping (Fig. 34, No. 12, 13). On the other hand, the secretory ducts running cephalad are arranged into three clusters on each side in the anterior trunk somites (Fig. 33, No. 4), as will be discussed below. Their orifices are restricted exclusively to the head region.

We will now follow such a cluster of secretory ducts over its entire length to the associated gland cells.

In the distal sector of the cluster (Fig. 38, No. 63), no gland bodies are found, only ordinary epithelial cells which lie between the secretory ducts of the glands and whose nucleus and protoplasm have a structure that looks identical to that of the cells of the skin epithelium. These apparently are the cells that migrate from the skin epithelium and gradually extend further and further between the secretory ducts of the glands. Even at a very slight distance from the distal end of the cluster, such cells occur very rarely. Here and there in the mid section of the cluster area the first stages of a transformation of these elements into true glandular cells are encountered

(Fig. 36, No. 35)[1]. Either between the secretory ducts (aup) or directly on them in the mesenchyme are elements (gdz_1) which are only slightly larger than the ordinary skin epithelium cells. However, their nucleus contains coarser chromatin granules and 2-3 chromatin globules, and their protoplasm, which forms a thin layer surrounding the nucleus, stains very deeply. The secretory duct projects distally from the cell; it is filled with a colourless, transparent secretion. This is therefore a typical gland cell.

The closer we come to the proximal end of the cluster, the rarely we encounter such gland cells between the secretory ducts, and in the end they are absent here altogether. A few cells can still be observed, but these are amoebocytes (am) of the mesenchyme which occur here and there over the whole extent of the cluster either on its surface or sometimes inside the cluster, having intruded between the secretory ducts of the glands from the surrounding body mesenchyme. Well-formed mesenchymatous marginal layers have apparently not developed around the clusters of secretory ducts; they are also absent in the associated gland cells.

Even closer to the proximal cluster end, elements (gdz_2) of ever larger proportions appear in place of the small gland cells. These cells are already found in the body mesenchyme, but in close proximity to the associated cluster of secretory ducts. As the cell becomes larger, so does the nucleus, and the number of chromatin granules and globules increases. As mentioned, the colourless, transparent glandular secretion at first occurs only in the secretory duct, not in the protoplasm itself.

If we compare one of the very largest of such gland cells (gdz_3) with the adjacent gland elements of a given cluster (Fig. 36, No. 35), the further development of this cell can be readily visualized.

In it the colourless, transparent secretion begins to form not only in the secretory duct, but also in the immediately adjacent sector of the protoplasm. The process continues; the secretion collects in a gradually increasing amount until it fills the protoplasm in the entire cell body (gdz_4), while the cell enlarges up to 300 μ in diameter. The oval or roundish nucleus does not change its structure and becomes only slightly enlarged.

---

[1] In the further description, the author always refers to this illustration which contains all phases of the gradual development of gland cells. As will be seen, these cells differ only in size from one body section to another.

Its diameter is now about 150 µ. As the collection of secretion increases, the cell protoplasm can be stained much less, but does not lose its finely granulated structure.

Gland cells which have thus reached the peak of their development are generally seen individually at the proximal end of the cluster of secretory ducts.

In the further course of the secretion process the cell (gdz_5, gdz_6) appears to become "exhausted". The nucleus becomes smaller, and accordingly its chromatin granules group closer together inside it. The protoplasm loses its finely granulated structure, becoming coarser and staining more deeply. It collects at the periphery of the cell, while the entire space around the nucleus is filled with a dense mass of secretion which contains only a few strands of protoplasm. The dimensions of the cell itself become smaller, and the secretion, too, is undergoing changes: it can now be stained with hematotoxylin.

At last the cell shrinks (gdz_7) to a relatively small size and seems to be completely filled with secretion that can be slightly stained with hematoxylin. The latter contains protoplasm remnants in the form of deeply staining compressions without any trace of structure. The cell centre is occupied by the nucleus which is usually still oval or spherical, although it is occasionally of irregular contours. It almost always stains homogeneously and very deeply, since it is filled with coarse chromatin granules.

Thus the gland cell has reached the end phase of its activity; it has already begun to degenerate and seems to be without further viability.

We have now followed the entire development of a giant gland cell of the inner body mesenchyme of *Acanthobdella*, having chosen a cell from the vicinity of the proximal end of a certain cluster of secretory ducts. All other gland cells belonging to the same cluster behave in very similar fashion, except that cells remaining further away from the distal end sector of the cluster – while undergoing exactly the same development – reach smaller and smaller dimensions. Thus it is found that the maximum size of cells in the mid preclitellar somites have a diameter of about 150 µ with the nucleus reaching a diameter of about 80 µ, while the elements in the mid head somites usually only reach a diameter of up to 50 µ with a nucleus whose diameter reaches about 25 µ. Thus the further the cell moves from the skin epithelium in which it originates, the larger it can become before the mass of its protoplasm stops to increase and before the secretion begins to accumulate in the cell body itself.

In addition to *Acanthobdella*, similar giant gland cells of the inner body mesenchyme are found in *Hemiclepsis marginata* and in the Ichthyobdellida. The author has not encountered them in the other Hirudinea or in the Oligochaeta.

Now we must examine those formations which occur only in the clitellar somites.

In the *Acanthobdella* specimens examined by the author, the skin epithelium of this body region generally resembles that of the others: the only difference is that here and there the ordinary skin epithelium cells form botryoidal masses which in the mesenchyme lie mainly between the longitudinal muscles and advance as far as the inner body mesenchyme without, however, invading the latter. Only rarely do the cells, which are distally embedded in such masses, border directly on the skin epithelium elements and project between the latter. For the most part, the botryoidal cell mass is sharply delineated from skin epithelium and is connected with it only through a fine, long base that is in fact merely a continuation of the mesenchymatous marginal layer below the skin epithelium. In the distal section of such a cell accumulation, the elements do not differ from the ordinary cells of the skin epithelium. However, their character changes toward the inner body mesenchyme: they become larger, their protoplasm stains more deeply, the nuclei assume a spherical shape and become larger, and instead of the usual 2 chromatin globules in the nucleus, there are now 3-4.

These are apparently formations that are homologous to the clitellar glands which occur in almost all Oligochaeta and Hirudinea. However, in the *Acanthobdella* specimens examined by the author, these glands are only in the initial stages of their development. This is probably connected with the fact that in the author's specimens the female genital apparatus was also not yet completely developed, as will be discussed below.

6. The coelom

The description of the situation in the coelom of Acanthobdella, provided by A. KOWALEVSKY (1896) is generally quite accurate. He wrote as follows (p. 267): "L'Acanthobdella possède un coelome divisé par une série des dissepements correspondant au nombre des somites. La cavité du corps contient tout l'intestin, la chaine nerveuse, et la vaisseau dorsal et ventral ... La cavité du corps est bien développée, elle possède une couche de cellules épithéliales qui recouvrent l'intestin, et contiennent dans leur intérieur des granules verdâtres – on peut les comparer aux cellules chlorogènes des oligochètes. Dans la paroi extérieure de la cavité du corps on ne distingue pas aussi facilement les cellules, mais pourtant on remarque les noyaux placés à une certaine distance l'un de l'autre, ce qui indique la présence d'une couche épithéliale. Dans la communication du mois de juin, j'ai dit que les organes génitaux sont placés dans la cavité du corps, ce qui est juste seulement relativement aux ovaires et aux oviductes, tandis que les glandes mâles sont placés dans les parois du corps et forment seulement des proéminences dans le coelome".

As this brief description indicates, the coelom (c) of *Acanthobdella* actually has characteristics that are typical for Chaetopoda. In each somite of the body it consists of a more or less wide cavity (Fig. 33, No. 3-5; Fig. 34, No. 10) that is bordered by the intestine, the dissepiments and the body wall.

These characteristics seem to be best developed in the preclitellar somites (Fig. 33, No. 4, 5; Fig. 41, No. 106), where because of the absence of seminal vesicles the body wall is relatively thin and the intestinal section not very voluminous. Here the coelom forms a broad cavity around the intestine (oe, d) in which medially the dorsal (dg) and ventral (vg) blood vessels are situated; below the latter is the ventral cord (cn). Laterally the coelom of the 1st preclitellar somite (c_6) projects only slightly (Fig. 33, No. 4; Fig. 41, No. 106). In the 3rd preclitellar somite (8) this is more pronounced (Fig. 33, No. 5; Fig. 41, No. 106); here the lateral pouches (cs_8) of the coelom (c_8) point cephalad and project slightly between the lateroventral longitudinal muscle strands and the coelom wall of the 2nd somite (c_7) – see Fig. 34, No. 7). Most significant seem to be the lateral coelom outpocketings (cs_7) in the latter somite (7) where they expand cephalad and project between the longitudinal musculature and the lateral coelom wall of the 1st preclitellar somite, advancing almost over that somite's entire length (Fig. 33, No. 4).

The dissepiments between the 1st and 2nd, 2nd and 3rd (Fig. 34, No. 7) preclitellar somite and that between the 3rd preclitellar and 1st clitellar somite are formed quite similarly (Fig. 41, No. 106, dsp). Each forms a rather thick mesenchymatous layer which connects the intestinal mesenchyme with the inner body mesenchyme. Dorsally as well as ventrally, the dissepiment layer is perforated by a wide opening (e. e_1), so that the dorsal and ventral sections of the coelom continuously project through the dissepiments. This characteristic can be regarded in a sense as a preliminary stage in the development of the ventral and dorsal coelomic sinus in the other Hirudinea, where the dorsal coelomic sinus contains the dorsal vessel, the ventral coelomic sinus the blood vessel and the ventral cord.

In the dissepiments, muscle fibres extend from the intestine to the body wall, as do the dorsoventral muscles. Thus one muscle cell each (dsz_1) extends from the lower intestinal quadrant; its proximal end ramifies at the intestinal wall, and its distal end attaches itself to the skin epithelium near the median line. Dorsally, 2 such cells (ds_7), which ramify at the upper quadrant of the intestinal wall, extend on each side, one of which inserts itself at the skin epithelium near the dorsal median line, while the other curves around the dorsal coelomic sinus, and ends between the longitudinal muscles after crossing the associated cell on the other side with its terminal rami. In addition, in each dissepiment a dorsoventral muscle cell runs close to the intestine; it attaches itself dorsally and ventrally at the paramedian line of the body, at the integument of the 4th somite annulus.

The coelom characteristics just described change very significantly in the clitellar somites, and this is most evident in the 1st clitellar somite (9); see Fig. 33, No. 6. Here the ventral coelom section (c_1) that encloses the ventral vessel (vg) and the ventral cord (cn) become separated from the rest of the coelom by a rather thick mesenchyme layer. It forms a wide tube that immediately follows the ventral perforation of the dissepiment between the 3rd preclitellar and the 1st clitellar somites. Thus the ventral coelom section in the 1st clitellar somite has changed into a true ventral coelomic sinus which is very much homologous to that in the other Hirudinea.

The lumen of the mid coelom section that surrounds the intestine on all sides, is reduced to a bare minimum (Fig. 33, No. 6; Fig. 39, No. 83-85; Fig. 41, No. 106) and completely filled by a cell layer (ct*) which here and there is traversed by mesenchyme strands (ms_1). Only rarely some insignificant cleavages can be observed (Fig. 39, No. 85) which divide the cell mass into 2 epithelial layers and which here represent the last remnants of the coelom. Laterally the coelom section in question borders directly on the wall of the adjacent testes (h), with whose cavity it communicates over a varying distance (h_1); this will be discussed below. Between it and the testes, no dorsoventral or diagonal muscles intrude; they all extend laterally of the testes. Dorsally the above named coelom section unites with the coelom (c) that encloses the dorsal vessel (dg). The coelom forms a wide cavity that follows the dorsal perforation of the dissepiment between the 3rd preclitellar and the 1st clitellar somites. Since it borders laterally on the reduced coelom section that surrounds the intestine and thus appears completely enclosed, it (as the corresponding ventral space) can also readily be compared with the dorsal coelomic sinus in the other Hirudinea.

The coelom of the 2nd clitellar somite (10) represents an intermediate stage (Fig. 34, No. 8) between the characteristics in the just described and those in the ordinary trunk somite of *Acanthobdella*. Although the ventral coelomic sinus (c_1) of the 1st clitellar somite also remains separate in the 2nd somite, it does in places unite with coelom section (c) which surrounds the intestine and which here already forms a well-developed albeit narrow cleavage around the intestine. Dorsally the latter section continues directly into the dorsal coelom section that is developed as usual. The dorsoventral muscles, which run between the coelom wall and the testes, are already present in the 2nd clitellar somite; ventrally they insert either at the ejaculatory duct and the atrium of the male genital apparatus or at the vagina, i.e. their points of attachment have shifted toward the somite margins. Dorsally, however, they are attached as usual at the integument near the paramedian line of the body.

The dissepiment between the 1st and 2nd clitellar somite is developed as the above described dissepiments of the preclitellar somites. The only peculiarity is that the atrium of the male genital apparatus – because it lies on the ventral median line – is embedded in the ventral perforation of the dissepiment, and the corresponding coelomic sinus surrounds the atrium and the ejaculatory ducts which lead into the coelomic sinus. Between the ejaculatory ducts lie the ventral blood vessel and the ventral cord.

The following dissepiment (Fig. 34, No. 9) which separates the 2nd from the 3rd clitellar somite, shows a peculiar characteristic that differs from all other dissepiments and resembles those less than it does a typical Chaetopoda dissepiment. Only ventrally (Fig. 40, No. 92) does it have a small perforation (c_1) in which the ventral vessel (vg) and the ventral cord (cn) lie; over the entire remaining distance, however, it forms an uninterrupted layer which completely separates the coelom sector of the 2nd clitellar somite (situated laterally and above the intestine) and the coelom sector of the 3rd clitellar somite (11). Thus the dorsal blood vessel (dg) perforates this dissepiment directly without the presence of an open coelomic sinus around it.

Behind the dissepiment the ventral coelomic sinus gradually widens to receive the ovaries, and then it unites with the dorsal coelom sector. The latter begins behind the above mentioned dissepiment as a space containing the dorsal vessel, and it surrounds the dorsally rising upper parts of the ovaries, so that the latter now appear to be surrounded on all sides by the coelom in which they extend caudad near the dorsal median line above the dorsal vessel.

In the posterior section of the 3rd clitellar somite (11), the coelon is already formed in the manner typical for the mid trunk somites. In the latter (Fig. 34, No. 10) it forms a more or less developed cavity around the intestine, slightly widened dorsally where it contains the ovaries (ov) and the dorsal vessel, and ventrally where the ventral vessel and the ventral cord are situated; thus the coelom suggests a ventral and dorsal sinus in these somites, where insignificant lateral coelom outpocketings (c*) occur as well.

The dissepiment between the 3rd clitellar somite and the 1st mid trunk somite (12) and all following dissepiments of the mid body (Fig. 34, No. 11) constitute fairly thin mesenchymatous layers (ms*) which united the mesenchyme of the intestine with the inner body mesenchyme (Fig. 37, No. 39). They have dorsal (c) and ventral (c_1) perforations. As described above for the preclitellar somites, the muscle cells in them occur at the rate of 2 on each side dorsally (dsz) and 1 or usually also 2 ventrally (dsz_1), but one of the latter appears to be poorly developed. In addition, 2 or 3 dorsoventral muscle cells (dvm) occur in the dissepiments, as mentioned in the description of the musculature.

The dissepiment (dsp_{19}) that separates the last mid trunk somite (19) from the 1st somite of the hindgut region (20) is situated in the 4th annulus of the 8th mid trunk somite (Fig. 41, No. 109) and is thus somewhat shifted cephalad. The structure of this dissepiment shows only insignificant deviations from the above mentioned. It contains on each side 2 dorsoventral, 2 dorsal and 2 ventral muscle cells extending from the intestine to the integument; its ventral perforation is well-developed, while the dorsal perforation is very poorly developed, and its walls are usually directly accumbent to the dorsal vessel. The coelom (c) of the 1st (20) and all 5 following somites of the hindgut region forms only a very narrow cavity around the intestine in which a widening (c_1) occurs ventrally (Fig. 39, No. 71). The dorsally widened section can hardly be distinguished here (Fig. 39, No. 71).

In the 1st somite of the hindgut region (20) the coelom (c_{20}) occupies only the anterior part of the somite, and in its middle the next dissepiment is already present (Fig. 41, No. 108 dsp_{20}). The coelom thus forms a cavity that is much smaller than in the mid trunk somites. The dissepiment is developed as the previous one, i.e. its dorsal perforation is also very poorly developed. It can be seen that this dissepiment has undergone a secondary forward shift from its original position on the margins between the 1st and 2nd somites of the hindgut region: its characteristic ventral (2 on each side) and dorsal (also 2 on each side) muscle cells attach to the integument only in the 4th annulus of the 1st somite, to which they extend in the inner body mesenchyme.

The dissepiment (dsp_{21}) that separates the 2nd somite (21) from the 3rd (22) is situated between the 1st and 2nd annuli of the 2nd somite of the hindgut region (Fig. 41, No. 108). It is formed as the dissepiment just described. Thus the coelom (c_{21}) of the 2nd somite occupies the posterior section of the 1st somite (20) and only the 1st annulus of its own somite (21), i.e. it is reduced in size as is the previous one. However, the corresponding dissepiment suggests its original position: the ends of its ventral and dorsal muscle cells (2 on each side) extend up to the 4th annulus of the 2nd somite, where they attach themselves.

The coelomic sinus (c_{22}) of the 3rd somite (22) occupies only the 2nd and 3rd annuli of the 2nd somite (21) of the hindgut region (Fig. 41, No. 108). The dissepiment (dsp_{22}) between the 3rd (22) and 4th (23) somites lies in the 4th annulus of the 2nd somite. Its dorsal (here only 1 on each side) and ventral (2 on each side) muscle cells attach themselves in the 2nd annulus of the 3rd somite and have thus also shifted cephalad, although this phenomenon is not very pronounced.

The coelom (c_{23}) corresponding to the 1st somite (23) occupies the 4th annulus of the 2nd somite (21) and the 1st annulus of the 3rd somite (22), i.e. it is considerably reduced and shifted forward by almost a whole somite. The dissepiment (dsp_{23}) which separates the 4th somite (23) from the 5th (24) is in the 2nd annulus of the 3rd somite (22), It appears more poorly developed than the previous ones, since it contains on each side only one dorsoventral, one dorsal and (as usual) two ventral muscle cells. The dorsal and ventral muscle cells characteristic for the dissepiment attach themselves to the body wall as early as in the 1st annulus of the 4th somite and have thus considerably shifted forward. Their true relationships can only be determined by comparing them with the dissepiments described earlier.

The following coelomic sinus (c_{24}) assigned to the 5th somite (24) of this region occupies the posterior section of the 3rd somite (22) of the hindgut region and has therefore shifted cephalad even more than its predecessors. The dissepiment (dsp_{24}) between this and the 6th somite (25) lies between the 3rd (22) and 4th (23) somite. The hindgut region therefore has either no dorsal dissepiment muscle cells at all or only one cell on each side which then attaches with one end to the intestine near the dorsal median line, with the other end – curving around the intestine – to the body wall near the ventral intermediate line. Only the 2 pairs of ventral muscle cells of the dissepiment are well-developed here.

The coelom section (c_{25}) corresponding to the 6th somite (25) occupies almost the entire 4th somite (23) of the hindgut region. Here the two branches of the dorsal blood vessel in the somite descend from the median line of the intestine to its lateral line. The coelomic sinus of the 6th somite surrounds these vessels which advance further to enter the inner body mesenchyme. In the vicinity of the posterior margin of the 4th somite of the hindgut region the last dissepiment (dsp_{25}) of the coelom is situated. It forms a mesenchymatous layer on each side (Fig. 34, No. 13) which reaches only from the lateral line of the intestine to the ventral coelom sector (c) because the intestine (hd) here already merges into the inner body mesenchyme. However, even in this formation a dissepiment can be clearly observed, for the 2 pairs of characteristic muscle cells (dsz_1) are very well formed ventrally in the layers on both sides. Here the dorsal and dorsoventral muscle cells are either completely absent, or represented by the muscle cells extending radially from the intestine to the body wall. 3 such cells occur on each side; they are quite poorly developed. One extends dorsad, the 2nd laterad, the 3rd ventrad.

Behind this dissepiment, the coelom (c) in the 5th and 6th somite of the hindgut region forms an oval, pouchlike widening (Fig. 34, No. 14; Fig. 35, No. 16; Fig. 41, No. 108) in which the anal ganglia system and the ventral blood vessel (vg) with its branches are situated.

This description shows that the 6 somites of the hindgut region are reduced and shifted cephalad in terms of their coelom sections. This is confirmed by the characteristics of the dissepiments. In this respect we can obtain important information from facts obtained by examining the intestine, which will be discussed below. In this context it should only be mentioned that the positional changes of the dissepiments and the reduction of the corresponding somite cavities are caused by the cephalad shift of the corresponding intestinal sectors.

Finally, the comments by A. KOWALEVSKY (1896, p. 269) should be cited here: "Le canal intestinal est attaché aux parois du corps par vingts paires de dissépiments correspondant au nombre des segments". This is correct if we disregard the dissepiments of the head region.

Let us now briefly examine the characteristics of the coelom in the other Hirudinea.

It is common knowledge that the reduction of the coelom's central section and the strong development of its peripheral section is characteristic for Hirudinea.

In Rhynchobdellidae the reduction of the central coelom section leads to a formation where the segmentally arranged coelomic compartments are replaced by longitudinal dorsal and ventral coelomic sinuses, connected with each other by insignificant channels. In Gnathobdellidae the dorsal and ventral coelomic sinuses as well as the connecting channels are reduced to a minimum. In the Herpobdellae the dorsal coelomic sinus is completely absent. This is all caused by the extremely strong development of the mesenchyme which is situated around the intestine, in the dissepiments and outside the coelom. In this connection, O. BÜRGER (1902) wrote: "The retrogression of the coelom takes place in particular at the expense of the lateral cavities and is caused primarily by the enormous strengthening of the septa".

The development of the peripheral coelom sections, however, is particularly evident in the formation of the two lateral coelomic sinuses and the hypodermal coelomic lacunae as well as the corresponding connection channels. The highest degree of development in the peripheral coelom section is found in the Gnathobdellidae, where the lateral sinuses are formed in the fashion of true blood vessels, and where the hypodermal coelomic lacunae are extremely numerous.

This is apparently the outcome of a succession of functional changes that have occurred: in the Gnathobdellidae the true blood vessel system has completely disappeared and has been replaced by the highly developed peripheral coelom. In this respect the author quite agrees, on the basis of his own observations, with L. CUÉNOT (1891, p. 459) and A. OKA (1902) and therefore disregards the contradictory statements by BÜRGER (1891, 1894) about the vascular development in Gnathobdellidae, since in the author's opinion they require further confirmation.

This brief overview of the coelom situation in typical Hirudinea clearly shows that the coelom of *Acanthobdella* is considerably different and in this respect much closer related to the Oligochaeta who possess a well-developed coelom. However, by and large, the peculiar changes which characterize the coelom of the Hirudinea are already indicated in *Acanthobdella*. The dissepiments are quite voluminous and richly endowed with mesenchyme. The ventral and the dorsal coelomic sinuses are developed, although their full differentiation occurs only in the 1st clitellar somite. The author believes that the lateral coelomic sinuses can be compared with the coelom outpocketings in the 2nd and 3rd preclitellar somites. A major difference is the absence of any coelom processes that could be compared with the hypodermal coelomic lacunae that are characteristic for Hirudinea.

Thus the structure of the coelom in *Acanthobdella* represents an early stage that can be regarded as an ancestral form of the coelom in Hirudinea. However, the coelom in that genus conforms so absolutely to the coelom of Oligochaeta that *Acanthobdella* differs in this respect far more from all other Hirudinea than from the Oligochaeta.

Yet the structure of its dissepiment musculature is completely typical for that of Hirudinea. According to F. SCHMIDT (1903) similar characteristics are found in *Branchiobdella*, which belong to the Oligochaeta.

The coelom of *Acanthobdella* is lined on all sides with coelothelium which also covers all organs lying within the coelom.

This epithelium (ct) consists of a very delicate membrane that appears as a line in section and which is closely accumbent everywhere to the mesenchymatous marginal layer (Fig. 36, No. 26, 37; Fig. 37, No. 38-43; Fig. 38, No. 54, 56, 59, 62-68; Fig. 39, No. 71, 72, 76, 77, 83, 88, 89; Fig. 40, No. 92). Quite far apart from each other in this membrane are the nucleate cell sections (ct*) of the coelomic epithelium which usually project into the coelom (c), more rarely into the inner body mesenchyme (ms). In sections one sees a spindle-shaped proliferation of plasm, about 15-20 µ in width and 40-45 µ in length. The protoplasm is very finely granulated and stains very deeply. The oval vesicle-like nuclei contain a number of more or less delicate chromatin granules. The larger diameter of the nucleus is 25-30 µ, the smaller 15 µ. It usually contains 2-3 nucleoli.

A. KOWALEVSKY (1896, p. 269) wrote in connection with the coelothelium that forms the intestinal lining: "Les parois de l'intestin sont recouvertes, du côte de la cavité du corps, par une couche de cellules contenant des granulations vertes dans la partie recouvrant l'intestin médian. Cette couche de cellules correspond aux cellules chlorogénes des Oligochètes. Ces sellules absorbaient les sels de fer comme le font des cellules chlorogénes des Oligochètes". F. GRUBE (1851) already wrote that "the intestinal wall was largely surrounded by an apparently glandular tissue".

Indeed we find over the entire length of the midgut and hindgut (Fig. 33, No. 5, 6; Fig. 34, No. 8, 10; Fig. 41, No. 106) not the described peritoneal cells, but an uninterrupted layer of peculiar coelothelial cells (Fig. 36, No. 36, 37; Fig. 37, No. 38-40; Fig. 38, No. 68, 70; Fig. 39, No. 71, 83 clz).

They sit close together on the outer marginal layer of the intestinal mesenchyme (ms). Their shape varies greatly. One sometimes sees more or less flattened, oval cells (Fig. 36, No. 36; Fig. 38, No. 68, 70), and all transitional forms toward spherical and pear-shaped cells (Fig. 36, No. 37; Fig. 37, No. 38-40; Fig. 39, No. 71, 83); the latter attach themselves to the marginal layer by their trunk. The nuclei are usually round with a diameter of about 6-8 μ; they contain small chromatin granules and 1-2 nucleoli. The spherical cells have a diameter of 12-16 μ. The protoplasm consists of a fine framework that stains very faintly; the appearance of the cell bodies is granular only at the distal periphery.

In the protoplasm framework of the cells numerous granules are embedded that can be stained black with osmic acid (Fig. 38, No. 68, 70): they are absent only in the peripheral, finely granulated layer. When other fixing agents are used, such as alcohol, sublimate, sublimate glacial acetic acid, or picric acid, these droplets of the fatty substance disappear and are replaced in the protoplasm by small vacuoles. The fatty content of the cells can vary greatly. In the anterior part of the midgut are cells which contain few fatty droplets in comparison with those in the following sections. Cells which have been somewhat displaced by adjacent elements also have a smaller number of these droplets. Apart from these droplets, the author found no other embedded material in the described cells. Since he did not examine any live cells, he cannot determine the nature of the "granulations vertes" described by A. KOWALEVSKY. They may be none other than the above mentioned fatty droplets.

Occasionally typical mitoses are present in the described cells (Fig. 36, No. 36).

Only rarely can the above elements be observed floating freely in the coelom (Fig. 37, No. 40; Fig. 39, No. 83); in those cases they probably represent a few cells torn off this layer. Finally, the coelom section surrounding the intestine in the 1st clitellar somite is almost completely filled with such cells (Fig. 39, No. 83-85), but they do not contain any fatty inclusions there.

A. KOWALEVSKY (1896) regarded these elements as chloragogen cells. Their general position and structure, and their ability to absorb ferrous salts (discovered by KOWALEVSKY) definitely confirm this opinion, as does the fact reported by G. SCHNEIDER (1896, p. 386) that the chloragogen cells of Oligochaeta also contain a fatty substance. Although many other authors have denied that the chloragogen cells in most Oligochaeta show such characteristics, L. CUÉNOT (1891, p. 471) has confirmed them in *Branchiobdella*, and J.P. MOORE (1895) in *Bdellodrilus*. We therefore must recognize that the cells in question found in *Acanthobdella* are indeed homologous to the chloragogen cells of Branchiobdellidae and thus related to the chloragogen cells of the Oligochaeta in general. Not as closely related in this respect are the other Hirudinea where the so-called acid cells of Rhynchobdellidae and the botryoidal cells of Gnathobdellidae correspond to the chloragogen cells of the Oligochaeta, as demonstrated by A. KOWALEVSKY (1897). The location of these cells in the other Hirudinea does not resemble the relationships in *Acanthobdella*, and the reason for that is probably the peculiar development of the coelom in the former.

On the intestine, between the chloragogen cells, are cell bodies (Fig. 36, No. 37; Fig. 37, No. 38 rm*) resembling ordinary coelothelial cells which are scattered throughout the surface of the intestine in insignificant numbers. A closer examination of these cells shows that they are true epithelial muscle cells. In the basal section of each such cell, 2-5 fine muscle fibres (rm) are embedded that form the annular musculature of the intestine. These small muscle fibres extend through the basal parts of the chloragogen cells, closely accumbent from the outside to the outer marginal layer of the intestinal mesenchyme (ms); see Fig. 36, No. 37; Fig. 37, No. 38-40). At first glance it appears as if they had been generated by the chloragogen cells, but after close examination there is no doubt that they are associated with the above mentioned coelothelial cells. Over a certain distance, each muscle fibre is completely separated from the others, and only in the nucleate sector itself can 2 or 3 of them unite lengthwise by forming thin platelets of fibrillar-contractile substance.

Immediately following the dissepiment are 2 or 3 of the described muscle fibres (Fig. 37, No. 39) whose size seems to indicate that they are slightly more developed than the others. As usual, they originate in a coelothelial cell. Over a short distance they sometimes invade the intestinal mesenchyme, so that a muscle fibre embedded in the mesenchyme can be observed in the section. In this case it is very easy (by following this fibre a little farther) to determine how closely they are related to the coelothelial cell.

The same phenomenon occurs to a much greater degree in 2 muscle fibres (rm*) that follow the above described fibres (Fig. 37, No. 39, 40): both are embedded in the intestinal mesenchyme (ms) almost over their entire length, and it is only rarely observed that the fibre projects into a coelothelial indentation, extends over a short distance far outside the marginal layer of the intestinal mesenchyme, and then projects into the latter once again. Such fibres can also remain completely in the mesenchyme, and in that case we encounter a circular musculature which, lying inside the intestinal mesenchyme, has no relationship to the coelothelium, although its nature is definitely determined by the above mentioned transitional forms. The nucleate cell sections of these fibres very much resemble the other muscle cells of the body, since in one half of their periphery they have the fibrillar-contractile layer, while distad is their deeply staining, finely granulated prism with the chromatinous nucleus. The nucleate cell section is situated in the vicinity of the lateral line of the intestine. Toward both sides, the muscle fibre appears as a flat, U-shaped or almost ring-shaped fibre, i.e. structured as in the Hirudinea. Four such cells (2 on each side) form a type of muscle ring in the most anterior section of each somite, which is very characteristic. On the hindgut these muscle rings appear as sphincter-like formations that are set very deeply into the intestinal indentations.

The described coelothelial muscle cells represent a characteristic peculiarity of the splanchnic plate of *Acanthobdella*. Nothing comparable was discovered in the other Hirudinea. Because of the reduction of the coelom section surrounding the intestine, due to enormous mesenchyme development and coelom reduction, the annular musculature of the intestine has been shifted into the intestinal mesenchyme, and the splanchnic coelothelial layer for the most part no longer occurs as an epithelium covering the intestine on all sides distally.

In this respect, *Acanthobdella* resembles more those Oligochaeta whose annular intestinal musculature lies outside the longitudinal musculature, namely *Branchibdella* and *Haplotaxis* (syn. *Phreorytes*).[1]

In the coelom itself, i.e. in its protein-containing liquid, large numbers of free cells (cz) occur (Fig. 36, No. 36, 37; Fig. 38, No. 68; Fig. 39, No. 76). They usually consist of spherical elements with a diameter of about 10 μ, and they have a finely granulated protoplasm that stains faintly. Their nucleus contains few chromatin granules and 1-2 nucleoli; its diameter is about 6 μ. These cells never contain fatty granules as the above described chloragogen cells do. These circumstances as well as their habits prove with certainty that they do not have their origin in chloragogen cells. They usually contain small inclusions and quite resemble the free cells in the blood vessel system. In the free coelomocytes, mitoses are sometimes observed.

In addition to these elements, in exceptional cases the coelom may contain male genital products in various stages of development.

The author has never observed remnants of chaetae in the coelom of *Acanthobdella* as has been described various times in Oligochaeta.

7. The nervous system

A. KOWALEVSKY (1896, p. 269) commented briefly as follows on the nervous system of Acanthobdella: "Le système nerveux est composé 1) d'un ganglion sus-esophagien ou cerveau, 2) d'un amas gangliennaire sous-esophagien, 3) d'une chaine ventrale de ganglions et 4) d'un amas ganglionnaire postérieur ou de la ventouse".

Disregarding for the time being the supraesophageal, subesophageal and anal ganglion mass, we first proceed to decsribe the ventral cord.

It lies freely in the ventral coelom section below the ventral vessel (vg) and is formed by well differentiated ganglia (gn) and connectives (cn), as in the other Hirudinea (Fig. 33, No. 1, 3-6; Fig. 34, No. 7-13, Fig. 40, No. 92). The ganglia are usually in the mid section of the somite in question

---

[1] Cf. the author's article "The intestinal musculature of the Oligochaeta and Hirudinea" in Zoologischer Anzeiger, V, 27, 1904.

(Fig. 40, No. 97), and only in the somites of the hindgut region have they more or less shifted cephalad.

In regard to the total number of ganglia in the ventral cord of *Acanthobdella*, A. KOWALEVSKY (1896, p. 269) wrote: (behind the subesophageal ganglion mass) "suivent 4 ganglions éloigués l'un de l'entre à d'assez grande distance et réunis par de connectifs: puis vient le grand ganglion qui est placé entre les ouvertures mâle et femelle des organes génitaux ... Entre l'ouverture extérieure femelle et l'amas ganglionnaire postérieure on de la ventouse il y à encore 15 ou 16 ganglions ce qui dépend si on réunit ou ne réunit pas à cet amas le dernier petit ganglion de la chaine gangli [illegible] cord [illegible] situated anteriorly of the female genital opening, the 1st of which is close to the subesophageal ganglion mass; behind this opening are 13 ganglia or 14 – if we want to regard a ganglion shifted very close to the anal ganglion mass as the last free ganglion. Thus A. KOWALEVSKY's observations prove to be inaccurate.

Where the ganglia are situated, the ventral cord borders directly on the inner body mesenchyme (ms), and the ventral sectors of the ganglia project into the latter. As a rule, this is not very pronounced (Fig. 37, No. 41; Fig. 40, No. 90), but in the 3 clitellar somites the ganglia seem to be intruding half-way into the mesenchyme (Fig. 37, No. 42). It can therefore be observed that the ganglia are ventrally without the outer layer of the sheaths of the ventral cord which is formed by a fine lamella of the ordinary coelothelium (ct). At the margin between the ventral and lateral ganglia surface, the peritoneal epithelium forms a fold, rising on the one hand over the ganglion and continuing on the other hand on the parietal wall of the coelom.

The inner layer of the sheaths of the ventral cord (Fig. 37, No. 41-43; Fig. 40, No. 98, 99) consists of the neurilemma which is none other than the typical transparent, jelly-like mesenchyme containing a few cells. This neurilemma layer is usually poorly developed; where the ganglia are situated, it merges directly into the inner body mesenchyme, as mentioned above.

Longitudinal muscle fibres (mf) are embedded in the neurilemma. In each somite they originate in only 2 muscle cells whose nucleate sections are symmetrically arranged on each side of the median line, near the corresponding ventral ganglia. They are ordinary muscle cells in which the nucleate section secretes the contractile-fibrillar substance over only part of its periphery. From each of these cells, two projections extend cephalad and caudad, one of which forms the muscle fibre that runs dorsally near the median line, while the other slightly diverts laterad and runs laterally in the neurilemma. This latter muscle fibre occasionally divides in two, and then 2 muscle fibres can be observed laterally. The projections of a given muscle cell reach cephalad from the nucleate section to the middle of the preceding ventral ganglion, and caudad to the middle of the ganglion that follows the nucleate section.

It can therefore be said that the muscle fibres in the neurilemma of *Acanthobdella* are quite poorly developed and originate from only 2 strictly metameric muscle cells. In this respect, *Acanthobdella* shows quite the same characteristics as the other Hirudinea, and the same applies to the neurilemmal and coelothelial layers. On the other hand, the structure of the musculature of the ventral cord in the Oligochaeta differs from that in *Acanthobdella*, although F. SCHMIDT (1903, p. 700) found the identical characteristics in *Branchobdella*. The ventral cord of *Branchobdella* is also clearly differentiated into ganglia and connectives, which, as is known, is not the case or only poorly developed in most Oligochaeta including the Haplotaxida.

The inner sector of the ganglion of the ventral cord is made up of the central fibre mass (cfm); see Fig. 37, No. 41, 42; Fig. 40, No. 99) which is none other than a widening of the trunks of the connectives in the area of the ganglion. From the outside, the central fibre mass is covered by a thin neurilemma layer that originates in the general neurilemma sheath of the ventral cord. In the central mass itself, the nerve fibres are embedded in neuroglia originating in 2 glia cells (gz). These cells, which quite resemble APATHY's "median star cells" in the other Hirudinea, lie directly below the neurilemma layer where they are arranged one after another on the ventral median line of the ganglion near its centre (Fig. 37, No. 41). Occasionally these cells are arranged almost symmetrically to the left and right of the median line. Transitional forms between the ordinary position and the latter arrangement can be found in large numbers. In the central fibre mass, the lateral fibres are not differentiated into separate groups, and the stems of the connectives in the ganglion are also poorly individualized: here the median nerve disappears completely. In section, the central fibre mass appears as a square with rounded corners.

The periphery of the ganglion consists of ganglion cells (Fig. 37, No. 41, 42; Fig. 40, No. 99) which are accumbent to the central fibre mass. They form 6 typically developed clusters (Fig. 40, No. 100), each of which possesses its own glia sheath that originates in a single multipolar glia cell (gz). This glia cell corresponds to the "star cell of the ganglion cell clusters" described by APATHY in the other Hirudinea. The individual clusters are quite clearly differentiated because they are separated from each other and from the central fibre mass by thin neurilemmal lamellae which peripherally merge into the general neurilemma of the ventral cord.

Two of the 6 ganglion cell clusters are accumbent ventrally (mp) and four (two on each side) are accumbent laterally (lp) to the central fibre mass. The lateral clusters form oval masses of ganglion cells whose processes enter the central fibre mass from the sides. Dorsad these clusters extend to the dorsal ganglion suface, ventrad to the ventral surface. The anterior lateral cluster (lp_1) on one side of the ganglion almost touches the corresponding cluster on the other side in the anterior ganglion sector, where the clusters extend somewhat further ventrally. The posterior clusters (lp_2) are in a completely lateral position. Ventrally in the ganglion, between the anterior lateral clusters and the anterior sectors of the posterior lateral clusters, is the anterior median cluster (mp_1), consisting of an oval mass of cells. The posterior median cluster (mp_2), which forms a relatively insignificant group of ganglion cells, extends as an oval mass between the most posterior sectors of the posterior lateral clusters and slightly protrudes behind the latter. The processes of the ganglion cells of the median clusters enter the central fibre mass along the ventral median line. Thus only the median sector of the dorsal ganglion surface remains uncovered by the ganglion clusters.

The ganglia of the ventral cord of *Acanthobdella* are therefore typical for the ganglia of Hirudinea, and in this respect they resemble particularly the ganglia of Glossosiphonida. A particularly typical characteristic is the development of the ganglion cell clusters. As is known, among the Oligochaeta, only *Branchiobdella* has a similar differentiation of the ganglion cell groups, but less pronounced than in the Hirudinea. In each ganglion of *Branchiobdella*, two well-developed ganglion clusters are situated on each side, but ventrally the ganglion cells are almost completely absent in the ganglion, and they can therefore not be differentiated at all into definite clusters.

Now a few words on the structure of the glia and ganglia cells of *Acanthobdella*.

The finely granulated protoplasm of the former (gz) does not stain very deeply (Fig. 37, No. 41), while it absorbs somewhat more colour in the ganglion cells (Fig. 37, No. 41, 42). The nuclei of these two cell types show a distinct difference. In the glia cells they reach a diameter of about 10-15 µ and contain a considerable number of coarse chromatin granules; in the ganglion cells on the other hand, only a few larger chromatin globules occur, while the chromatin in the remaining nuclear cavity is distributed in the form of extremely fine granules. The dimensions of the spherical, vesicular nuclei vary considerably in the ganglion cells. There are nuclei with a diameter of no more than 5 µ, while others reach a diameter of up to 25 µ.

3 pairs of nerves extend from each ganglion of the ventral cord of *Acanthobdella* (Fig. 40, No. 97, 100). The 1st pair (n_1) originates (as all others) in the transitional area of the lateral and ventral surfaces of the central fibres. It exits slightly cephalad of the margin between the anterior (lp_1) and posterior (lp_2) lateral clusters, i.e. about in the middle of the anterior median cluster (mp_1). The origin of the 2nd pair (n_2) lies somewhat further caudad of the described margin, i.e. at the posterior end of the anterior ganglion cell cluster; the 3rd pair (n_3) originates near the anterior end of the posterior median cluster (mp_2). Beginning at the lower angle of the central fibre mass (cfm) which appears in section as a square, all these nerves (n) extend ventrad, i.e. toward the ventral body surface, between the lateral (lp) and median (mp) clusters, where they somewhat indent the latter; they do not run laterad as is the case in all other Hirudinea. In this respect, *Acanthobdella* resembles *Branchiobdella*, the Haplotaxida, Lumbriculidae, etc., where the nerves take a similar course as they exit from the ganglia of the ventral cord.

Insignificant deviations from the described type are found in *Acanthobdella* in the ganglia of the preclitellar somites due to a more or less developed enlargement of the anterior median cluster, so that the latter projects quite far into the inner body mesenchyme. As a rule, in the clitellar somites the ganglion cell clusters are also already enlarged. A. KOWALEVSKY (1896, p. 269) wrote about this: "puis vient le grand ganglion qui est placé entre les ouvertures mâle et femelle des organs génitaux". The clusters of ganglion cells in the 3 described ganglia extend very far ventrad into the inner mesenchyme, but a characteristic peculiarity of these ganglia is that quite considerable accumulations (ap) of ganglium cells are formed at the roots of the middle pair of nerves (Fig. 37, No. 42). These groups of ganglion cells, however, are not homologous to the 6 clusters, since they do not possess separate neurilemmal and neuroglial sheaths. These two cell groups are directly accumbent to the nerve fibres of the middle nerves and the central fibre mass, and they are covered only by the sheaths of the latter. They project between the anterior median and lateral clusters into the inner body mesenchyme and cause quite a significant increase in the total number of ganglion cells in the ganglia. Such accessory groups of ganglion cells are not known in any of the other Hirudinea.

The connectives of the ventral cord of *Acanthobdella* (Fig. 37, No. 43; Fig. 40, No. 98) which under weak magnification appear in section as round strands, are formed by 2 thick lateral trunks (cn) and one median nerve (mn) that extends dorsally between them. This median nerve corresponds to Faivre' nerve in the Hirudinea, but it is very poorly developed in *Acanthobdella* (Fig. 40, No. 98), and it loses its independence several times when it merges over a varying distance with one or the other lateral trunk of the connective (Fig. 37, No. 43). Occasionally in some somites many degrees of differentiation can be observed in the median nerves.

Ventrally in each somite, each lateral trunk of the connectives contains one glia cell (Fig. 37, No. 43 gz) which is equivalent to the connective cells in the other Hirudinea: it is always situated in the first somite annulus. These cells are quite large, and in section they occupy almost half the corresponding connective trunk. Their structure is the same as that of the median glia cells of the ganglia.

Thus the structure of the connectives of *Acanthobdella* is characteristic for the type of connectives found in Hirudinea, and it differs from that of Oligochaeta in the complete absence of neurochords. As is known, neurochords are characteristic for Oligochaeta, particularly for Haplotaxida and *Branchiobdella*. However, S. APATHY (1897, p. 572) noted that he had been able to detect similar nerve fibres (one in each lateral connective trunk) in another Hirudinea, the genus *Pontobdella*,

We will now describe the peripheral nervous system of *Acanthobdella*.

After they leave the ventral ganglion and enter the inner body mesenchyme, the 3 pairs of nerves of a given ganglion run to the bottom right, curving mediad around the median longitudinal muscle strands of the corresponding side, i.e. toward the ventral median line of the body (Fig. 34, No. 8 sn, 10 rn_2). Below the median longitudinal muscle strands the nerves reach the margin between the longitudinal and diagonal muscles and at the same time deflect into the somite annuli in which they then continue (Fig. 40, No. 97 rn_1, rn_2, sn).

All described nerves (rn, sn) of *Acanthobdella* consist of finely fibrile bundles (Fig. 37, No. 45-51) in which the nerve fibres lie so close together that it is impossible to differentiate them individually; the character of the nerves can only be determined by examining their relationships to the different body elements. In this respect, *Acanthobdella* resembles the majority of Hirudinea, because among those, only the Hirudinidae have nerve fibres that are so clearly differentiated that the number and the character of all fibres making up a certain nerve can be determined in transverse section.

Along the margin between the longitudinal and diagonal musculature, the anterior nerve (rn_1) of the somite runs through the entire half of the 1st annulus and unites at the dorsal median line of the body with the corresponding nerve on the other side, although it is relatively thin even when it exits from the ganglion (Fig. 40, No. 97). Thus the 1st somite (I) contains a ring nerve which quite resembles the ring nerves in the other Hirudinea described by the author (LIVANOW, 1903). In the somite annulus, it forms an almost complete nerve ring which is interrupted only on the ventral median line of the body. As in the other Hirudinea, the connection with its ventral sections is formed not at the margin of the longitudinal and diagonal muscles, i.e. not peripherally, but centrally, facilitated by the central fibre mass of the ganglion of the ventral cord.

The described ring nerve has the character of a typical motor nerve: its fibres form the motor nerve endings on the longitudinal muscles. In well-prepared slides these endings can be readily seen as they follow the annular direction of the ring nerve in all muscle cells (Fig. 37, No. 44, 47). In the nerve originate fine fibres covered by a neurilemma sheath; where they reach the longitudinal muscle cell, their sheath of connective tissue merges into that of the muscle cell. Here the contractile-fibrillar layer of the latter forms a more or less well-developed slit in which the nerve fibre enters and thus directly touches the protoplasm of the muscle cell. With customary staining methods, the entire slit is filled with a substance that stains very deeply, and its appearance resembles that of the motor nerve endings in the other Hirudinea. This fully confirms the findings of S. APATHY (1897), according to which in Hirudinea the neurofibrillae enter the protoplasm through the fibrillar-contractile layer of the muscle cell, while a sizable, well-perceivable slit would not be formed. However, in a few cases the author was able to demonstrate structures in *Protoclepsis tessellata* which are quite identical to those in *Acanthobdella.*

Closer related to the ring nerves are some longitudinal muscle fibres which, as we will see, alone constitute the entire longitudinal musculature in the anterior head region, since the other muscle fibres do not extend that far (Fig. 40, No. 97 pmd, pmd_1, int, int_1, pmr, pmr_1, lb). In some muscle strands, these longitudinal muscle fibres constitute strictly separate groups. In approaching the described fibres (lm; Fig. 37, No. 45)[1], the ring nerve does not curve around them from outside, as do all the others, but becomes so closely accumbent to them that it looks as if it were pressed into the fibre. In the transverse groove which forms on the muscle fibre, motor nerve endings can usually be observed (Fig. 37, No. 47). In addition, the contractile-fibrillar layer is interrupted at the bottom of the groove, and thus the nerve touches the protoplasm of the muscle cell directly. The reduction of the contractile-fibrillar substance in the groove is expressed in various ways. Usually there is only a relatively insignificant lateral slit, although occasionally the contractile-fibrillar layer disappears over almost a quarter of the fibre section, so that for example on both sides of the nucleate section only an insignificant lamella remains of the peripheral contractile layer.

---

[1] Although No. 45 as well as No. 46 represents a posterior annular nerve, the author refers to this diagram when describing the anterior annular nerve, since the relationships in question are exactly the same in both annular nerves of the somite in *Acanthobdella.*

This characteristic is quite similar to that which the author found in the other Hirudinea (LIVANOW, 1903) in regard to the longitudinal muscle strands crossing the ring nerves. This resemblance is also reflected in in the structure of the muscle elements that are being crossed. Their nucleus always lies in a well-developed protoplasm proliferation whose contractile-fibrillar layer is always absent on the inside.

We will now take a somewhat closer look at the distribution of the relevant muscle cells in the above described longitudinal muscle strands (Fig. 35, No. 22).

In each, the dorsal (pmd) and the ventral (pmd_1) paramedian longitudinal muscle strand are 3 such cells (Fig. 37, No. 45): in the lateral strands the nucleus lies on the somite margin, in the middle strand it lies on the mid section of the somite. In these strands, the cells are situated at the lateral margin. 3 muscle cells showing a quite similar behaviour are present in each of the intermediate longitudinal muscle strands, where ventrally (int_1) the entire muscle strand consists of these cells alone (Fig. 37, No. 49 lm*), while dorsally (int) they are joined by an ordinary muscle cell in the middle of the bundle (Fig. 37, No. 47 lm). In each of the paramarginal strands, 2 of the described muscle cells occur. Both extend toward the median in the dorsal muscle strand (pmr; see Fig. 36, No. 28, lm*), and their nuclei lie in the vicinity of the somite margins. In the ventral strand (pmr_1; see Fig. 37, No. 50, 51, lm*), which has shifted considerably toward the lateral line of the body, the muscle cell situated on the median side shows the same relationships, while the lateral cell has its nucleus in the middle somite sector. Another such muscle cell (Fig. 38, No. 53 lm*) with a nucleus situated at the somite margin is in the longitudinal muscle strand that runs dorsally, close to the lateral line of the body.

In addition to the above cells, other longitudinal muscle cells can show a quite similar behaviour in relation to the anterior ring nerve, and this seems to be caused by the presence of larger slits in the contractile-fibrillar layer for the entry of the motor nerve endings. Such characteristics constitute a transition toward the typical behaviour. On the other hand, the longitudinal musculature contains muscle cells (mz*) which in terms of their structure are identical with the above described, but which are not closely related to the ring nerve (Fig. 35, No. 22). They will all be mentioned here, and this will complete the description of the longitudinal musculature. One such cell with the nucleus in the middle somite sector lies at the ventral median line. The nucleus of another such cell lies at the somite margin near the paramedian longitudinal muscle strand, and between the intermediate and paramarginal strand are 2 more such cells, whose nuclei lie at the somite margins. Dorsally and ventrally, 2 such cells are situated between the median line of the body and the paramedian longitudinal muscle strand, one of which has its nucleus at the somite margin, the other in the middle somite sector. Another such cell lies near the intermediate line; its nucleus is in the vicinity of the somite margin. Between the intermediate and the paramarginal muscle strand is another cell whose nucleus is in the middle somite sector; and finally, laterally of the paramarginal strand is one such cell whose nucleus is at the somite margin, and another cell whose nucleus is close to the lateral longitudinal muscle strand.

These facts indicate that the differentiation of the longitudinal muscle fibre system, which is connected to the ring nerves, is less pronounced in *Acanthobdella* in comparison with the system of longitudinal muscle strands in the other Hirudinea. In the latter the longitudinal muscle cells differ quite considerably from the other elements of the longitudinal musculature which are constructed according to the ordinary type of Hirudinea muscle cells; also the crossings of the ring nerves show a completely different picture than the well-differentiated motor nerve endings.

It should be added that one or the other muscle cell that is closely related to the ring nerves can be absent in the described longitudinal muscle strands or may at least not show such behaviour.

In the dorsal paramarginal and ventral paramedian longitudinal muscle strand, each ring nerve of the 1st somite annulus sends a nerve branch to the Oligochaeta muscle cells on which it apparently forms typical motor nerve endings.

The anterior ring nerve contains two types of cellular elements. The first are typical ganglial cells (gnz) which project into the inner body mesenchyme and form a ganglion at the lateral line (Fig. 40, No. 97). The latter usually consists of one large and 2 or more small cells which are accumbent to the former. Secondly, 2 or 3 medium-sized, bipolar cells are found here (nz). One of these is situated proximad on the nerve, always ahead of the ventral intermediate longitudinal muscle strand (int_1); the other two lie dorsally, on the median side of the paramarginal (pmr) or intermediate (int) strand. One or the other of these may occasionally be absent. They can all be differentiated in structure (Fig. 37, No. 46) from the ganglion cells: their protoplasm is lighter in colour, with a light edge, and their round, vesicular nucleus measures about 10 µ in diameter. The nucleus contains very small chromatin granules and a nucleolus. The described cells resemble most the nerve cells of the large nerve tubes in the other Hirudinea, and this also applies to their identical position. The presence of large nerve tubes was to be expected in *Acanthobdella* An important indication is also the circumstance that the author was able to find that the ring nerve was crossed by the above described muscle cells which certainly resemble the longitudinal muscle strands in the other Hirudinea and show a very similar picture in regard to the crossing of the ring nerve, which the author (LIVANOW, 1903) described in the other Hirudinea. This in the author's opinion proves without a doubt the existence of large nerve tubes in the ring nerves of *Acanthobdella*, although their histological differentiation still remains unsolved in our genus, since the author was unable to tell the individual nerve fibres apart.

The anterior ring nerve is accompanied over its entire length at the margin between the longitudinal and diagonal musculature by an annular muscle fibre (Fig. 37, No. 47, 48, rmf), which is formed by 2 symmetrically situated muscle cells. One such cell runs in one half of the body section; dorsally and ventrally it meets the corresponding end of the cell on the other side. The nucleate cell sector always lies at the lateral line of the body and, as the entire muscle fibre itself, always distad of the ring nerve. An interesting peculiarity of these cells are their short processes (rnf) which here and there detach themselves from the muscle fibre and migrate toward the skin epithelium. Each process begins with a wide protoplasmatic root, but at the periphery it has a thin fibrillar-contractile layer. Below the epithelium the process divides into a few delicate rami which project between the epithelial cells (Fig. 36, No. 24) and reach as far as the cuticula, where they finally disappear. These processes occur over the entire length of the muscle cell (Fig. 37, No. 47), even at its nucleate sector (Fig. 37, No. 48). The latter slightly projects distad, i.e. toward the skin epithelium, and here the contractile-fibrillar layer is absent on the epithelium side of the cell.

The structure of such muscle cells resembles primitive muscles such as the larval muscle cells of Polychaeta. On the other hand, they are quite homologous to those annular muscles that accompany the anterior ring nerve in the other Hirudinea. However, in the latter, the peripherad processes of the annular muscle fibres are either localized in certain areas, as in the Glossophonidae, where such processes occur only in the crossing of longitudinal muscle strands, or they are completely absent as in Hirudinidae, where only ordinary muscle fibres formed in Hirudinea fashion are present. Thus the primitive type of the described muscle cells of *Acanthobdella* has either changed or has been lost completely in the other Hirudinea.

Other characteristics are found in the middle nerve (su) of the somite of Acanthobdella which runs in the 2nd somite (II; see Fig. 34, No. 8; Fig. 40, No. 97).

It is a thick nerve which also extends over its entire length along the margin of the longitudinal and diagonal musculature. However, it does not constitute a ring nerve, since it dissolves into its smallest terminal rami in the vicinity of the dorsal median line of the body. In this respect, the described nerve resembles the middle nerve of the somite in the other Hirudinea. This similarity is also manifested by the fact that it consists exclusively of sensitive nerve fibres, and that it is thus the sensitive nerve of the somite of *Acanthobdella* Its rami innervate all sensory organs in the integument of the somite. The only one of these rami to attain some thickness is that which extends along the ventral paramedian line to the integument, all others seem to be less individualized and poorly developed.

Over the entire length of the middle nerve, small ganglion cells are found scattered here and there, without any regularity; they occur with particular frequency in the vicinity of the ventral ganglion and where the nerve branches start. Constant formations are 2 insignificant ganglia (Fig. 34, No. 8; Fig. 40, No. 97 gnz), one of which (Fig. 37, No. 49 gnz) is accumbent on the median side of the ventral intermediate longitudinal muscle strand (lm*), the other (Fig. 37, No. 51 gnz) is accumbent to the nerve at the lateral line of the body. The former ganglion is a club-shaped mass embedded in the inner body mesenchyme and usually consists of one large and several small ganglion cells. According to its position and structure, this ganglion is quite similar to the lateral ganglion in the other Hirudinea. The other above described ganglion is mounted nediad on the nerve and contains 2 large and one or more small ganglion cells. Its structure and position are identical to those of the ganglion of the anterior ring nerve. A KOWALEVSKY (1896, p. 268) wrote, probably referring to this ganglium: "Dans la proximité de ces grandes cellules (i.e. the diagonal muscle cells) j'ai trouvé des petits ganglions nerveux, qui envoyaient des nerfs vers la peau oú ils se terminaient dans des organes sensitifs". There is no doubt that the nerve branches extending to the integument near the ganglion in question start from the sensitive nerve, but the author never observed that the ganglion itself generated such rami.

The position of the two above mentioned ganglia on the nerve occasionally deviates slightly from the described typical behaviour, but it is rare that the ganglion cells (gnz) are separated from each other (Fig. 37, No. 51), namely one in a certain space between the longitudinal muscles, the other in the adjacent space.

It should be mentioned here that while the small ganglion cells in the described ganglia are quite identical with the cells in the ganglia of the ventral cord, the large cells of this type look somewhat different. Their finely granulated, deeply staining protoplasm usually contains peculiar inclusions which are almost impossible to stain and which look like globules or fibres. In the central (sensory) nerve of the somite of *Acanthobdella*, no other cellular elements occur that could be compared with the nerve cells of the large tubes (described for the anterior ring nerves). This fact is in full agreement with the behaviour which the author (LIVANOW, 1903) reported in the other Hirudinea, and it is an important indication of the true nature of the bipolar cells which in Hirudinea occur solely in the motor ring nerves.

The posterior nerve of the somite of *Acanthobdella* (Fig. 34, No. 10; Fig. 40, No. 97 rn_2) has the same dimensions as the anterior nerve and is considerably thinner than the middle sensitive nerve. It runs in the 3rd somite annulus (III) at the margin between the longitudinal and diagonal musculature and merges directly into the corresponding nerve of the other side at the dorsal median line of the body, i.e. it forms a posterior nerve of the somite. As the anterior nerve, it, too, is a typical motor nerve, and its fibres innervate all longitudinal muscles within its range. The same close relationships to certain muscle fibres shown by the anterior ring nerve are also found in the posterior ring nerve, only less pronounced. The author (LIVANOW, 1903) found similar characteristics of the posterior ring nerve in the other Hirudinea. As a rule, it is easy to find where the muscle fibres running dorsally are being crossed (Fig. 37, No. 45), although the picture is not always as clear and pronounced as with the anterior ring nerve. However, the crossings of the lateral and ventral muscle fibres are never very pronounced and can be absent altogether. As far as the cells of the posterior ring nerve of the somite are concerned (Fig. 37, No. 46 nz), the author refers to what has been said about the anterior ring nerve, since there is no marked difference between them in this respect. The posterior ring nerve has no accompanying annular muscle fibre, as the author has also reported in regard to the posterior ring nerve in the other Hirudinea (LIVANOW, 1903).

A peculiarity of the respective nerve in *Acanthobdella* is the existence of 2 nerve branches which do not occur in the anterior ring nerve (Fig. 40, No. 97). One of these branches (dn) separates from the nerve immediately after it leaves the ganglion of the ventral cord, runs in the inner body mesenchyme to the dissepiment between the above mentioned and the following somite, extends further into this dissepiment and finally reaches the mesenchyme layer of the intestine, in which it terminates. According to its origin and course, this branch of the posterior ring nerve is fully homologous to the dorsal nerve of the somite in the other Hirudinea, although in comparison it is very poorly developed, and this is the main difference between the neurosomite of *Acanthobdella* and that in other Hirudinea. Apparently this is a case of a more primitive condition, where the clear differentiation of a sensitive dorsal nerve has not yet taken place.

The other branch of the posterior ring nerve of *Acanthobdella* divides on the median side of the ventral paramedian longitudinal muscle strand (pmd_1) and extends into the 4th somite annulus (IV; see Fig. 40, No. 97). Here it runs along the margin of the longitudinal and diagonal musculature to the lateral line of the body, where it terminates by uniting with the subcutaneous lateral nerve (ln) that will be discussed below (Fig. 37, No. 52). The above mentioned nerve branch is clearly related to the ventral muscle fibre in the Oligochaeta; over its entire length it extends small fibres to the longitudinal muscles, where they form motor nerve endings. It also forms similar poorly developed connections with the above mentioned muscle cells of the ventral paramedian (pmd_1), intermediate (int_1) and paramarginal (pmr_1) longitudinal muscle strand, as the posterior ring nerve itself. Mediad of the intermediate muscle strand, this nerve branch has a bipolar nerve cell of the large tubes. This type of nerve branch was also described earlier by the author (LIVANOW, 1903) as characteristic for the neurosomite of the other Hirudinea. However, this branch is more developed in *Acanthobdella* and thus resembles the other principle nerves of the somite more than is the case in the other Hirudinea.

In addition to the described nerves, Acanthobdella also has a nerve (ln) which is known to be completely absent in the other Hirudinea. It is a lateral nerve that runs longitudinally along the lateral line of the body (Fig. 33, No. 4-6; Fig. 34, No. 7-13; Fig. 40, No. 96, 97). It lies directly below the skin epithelium, and it even impresses itself into the latter at the somite margins (Fig. 36, No. 27, 30).

The lateral nerve consists of a fine bundle of nerve fibres (Fig. 36, No. 27, 29, 30; Fig. 37, No. 51; Fig. 38, No. 53) which is covered by a well-developed mesenchymatous neurilemmal sheath. It usually does not contain ganglion or nerve cells. The lateral nerve is connected with the two ring nerves and the sensitive middle nerve of the somite through small branches, or it is directly accumbent to them over a short distance (Fig. 37, No. 50, 51 b). As mentioned, the nerve branch (hnz) of the 4th somite annulus enters the lateral nerve, where it terminates (Fig. 37, No. 52). The lateral nerve runs uninterruptedly through the entire somite and continues into the adjacent somites. Caudad the lateral nerve extends almost to the attachment disk where it gradually disappears. It is closely related to the annular (rm) and diagonal muscle cells (dm), being directly accumbent to the former (Fig. 36, No. 27, 29, 30; Fig. 37, No. 51a) and extending insignificant branches into the latter. In both cases the mesynchymatous neurilemmal sheath of the nerve or its branch merges into the mesynchymatous sheath of the muscle fibres, and the nerve fibres themselves ar so closely accumbent to the contractile-fibrillar muscle layer that a thin groove forms on the muscle fibre where it touches the lateral nerve. The above described nerve also directly leans against the nucleate sector of the diagonal muscle cell and the cell of the annular muscle fibre (rmf) that accompanies the anterior ring nerve (Fig. 37, No. 48). Since the author was unable to observe any relationship between the diagonal and annular muscles and the ring nerves of the somite, he is inclined to believe that the lateral nerve plays the role of a motor nerve for these muscles and that in addition it may contain sensitive fibres resembling the large nerve tubes.

After C. SEMPER (1876) had described the so-called "side line" in the Oligochaeta as a nervous formation, F. VEJDOWSKY (1884) examined these structures fairly thoroughly in many Oligochaeta and called tham "lateral ganglion cell strands". Mainly based on the studies of these two authors, others, such as B.F. BEDDARD (1895) and A. LANG (1894) also recognized the presence of a nervous side line in the Oligochaeta.

On the other hand, R. HESSE (1894) saw this as a primarily muscular structure and was inclined to regard only a small portion of it as perhaps a nervous formation; he wrote (1894, p. 402): "In *Tubifex*, *Fridericia galba* and *Lumbriculus variegatus*, I became convinced that a strong nerve bundle coming from the dorsal pharyngeal ganglion enters exactly into the side line ... It is probable that this nerve continues along the side line, although I was thus far unable to observe it there". HESSE therefore wanted to differentiate two different formations in the side line of Oligochaeta, the muscle cells and the nerves, although he later noted without qualification: "I have found no nerve that ran along the side line".

The majority of recent researchers have also expressed the view that the side line is in fact nothing but a row of the nucleate sectors of the annular muscle cells.

Following his detailed studies, M. BOCK (1901) thought that he could differentiate two different formations in the side line of Oligochaeta, but he interpreted them quite differently, namely as cell bodies of muscles, and a lymph vessel. The contents of that part of the side line that extends distally of the muscle bodies, he described as "une substance peu abondante, finement fibreuse" (p. 29, 30), but he claimed: "Cette matière fibreuse ne ressemble point à la substance ponctuée des nerfs ... je n'ai pu me convaincre de la prétendue innervation directe de la ligne latérale. Deux nerfs, il est vrai, partent de chaque côté du cerveau dans cette direction, mais c'est plutôt un peut au dessus de la ligne latérale qu'ils entrent dans le paroi du corps ... Je conclus donc de tout ce qui précède que ce nerf latéral n'existe pas".

As far as the corresponding formation in *Acanthobdella* is concerned, its histological structure and its relationships leave no doubt about its nervous character. Certainly, the mesenchyme may contain lymphatic spaces in the vicinity of the lateral nerve, but this is quite irregular and unimportant.

The facts pertaining to *Acanthobdella* seem to furnish indirect proof that the side line of Oligochaeta, too, must apparently contain a lateral nerve. However, while in *Acanthobdella* the nucleate sectors of the annular muscle cells are already completely separated from the above named nerve, the nucleate sectors of these cells seem to be still closely accumbent to each other, thus forming a uniform "side line". In comparison with the Oligochaeta, *Acanthobdella* would therefore represent a further step in the development of the side line.

Since the illustrations of M. BOCK (1901) strongly resemble the picture presented by the lateral nerve of *Acanthobdella*, they can to a certain degree confirm the above view. In addition, the author has himself examined the side line of Oligochaeta and found a formation that certainly by and large resembles the lateral nerve of *Acanthobdella*.

The above description of the neurosomite of *Acanthobdella* shows that it is by and large of the type which C. WHITMAN (1892), C. BRISTOL (1898) and LIVANOW (1903) found characteristic for the Hirudinea. Nevertheless, the difference between *Acanthobdella* and the Oligochaeta is not as important as it may seem at first sight. The structure of the ventral ganglion and the connectives may quite resemble that in the Hirudinea, but on the other hand, the exit of the nerves from the ganglion and the incomplete development of a concrete dorsal nerve of the somite is more reminiscent of the Oligochaeta. The presence of a lateral nerve in *Acanthobdella* falls in the same category. The course of the other nerves and their distribution in the somite is generally the same in both groups, although it has to be admitted that this question is at present not sufficiently researched as far as the Oligochaeta are concerned. We mainly have the description by F. BEDDARD (1895, p. 22, 23) who wrote: "The number of nerves given off in a segment varies considerably in different genera of Oligochaeta ... There is not much information as to the course of the branches after they have left the nerve-cord; ... the branches arising from the cord were continuous right around the body, apparently joining dorsally". R. HESSE (1894) wrote about Lumbricidae "that the sensory organs of each segment lie on three belts running around the segment ... the three sensory belts are associated with the three pairs of ring nerves arising in each segment from the ventral cord", and finally: "In *Lumbricus herculeus*, the anterior and posterior ring nerves, which are thinner than the middle nerve, remain over their whole length on the margin of the two muscle layers without entering the annular muscle layer. Perhaps they have mainly motor functions, while the middle nerve is perhaps largely sensory". This description by HESSE is enough evidence to judge the composition of the neurosomite of the Lumbricidae. It was supplemented by his report on the middle nerve: "about in the area of the intestine, the nerve leaves the marginal line between the longitudinal and diagonal muscle layers and gradually projects into the latter until it finally extends inside the same far peripherad". The studies by G. RETZIUS (1892) on the distribution of nerve fibres in the neurosomite of Oligochaeta also point toward the presence of a middle sensitive nerve and 2 other, largely motor nerves.

The above cited descriptions should suffice to justify the conclusion that the structure of the neurosomite in Oligochaeta is basically the same as in *Acanthobdella* and in the other Hirudinea.

8. The head region

Since the external morphology of the head region of *Acanthobdella* has already been discussed above, we will in this context look only at the relationships between the body wall, the nervous system and the coelom of this region.

The central sector of the nervous system in the head region consists (Fig. 33, No. 1; Fig. 41, No. 101, 102) 1) of an ordinary ventral ganglion (gn_3) whose main mass lies in the 3rd annulus of the 5th head somite (5) and which from there projects into the 4th and 2nd annulus, 2) of the subesophageal ganglion mass that occupies the 3rd and 4th head somite and the 1st annulus of the 5th head somite, and 3) the supraesophageal ganglion mass (obm) situated in the middle sector of the 3rd head somite. As this description indicates, the 1st ordinary ganglion of the ventral cord is very close to the subesophageal ganglion mass, so that the median clusters of both almost touch each other; the connectives, however, still look well-developed, and therefore the ventral ganglion of the 5th head somite can be clearly distinguished even macroscopically.

In comparison with the other Hirudinea, the subesophageal ganglion mass of *Acanthobdella* (Fig. 33, No. 1; Fig. 41, No. 101, 102) has a greatly elongated body which lies in the ventral sector of the coelom directly below the esophagus (oe). On both sides, the subesophageal ganglion mass generates a thick pharyngeal connective (scn) cephalad toward the supraesophageal ganglion mass (obm), while laterally it projects a few nerves (n_1, n_2, n_3, n_4) into the body wall.

The central fibrous part of the subesophageal ganglion mass is clearly differentiated lengthwise into 4 successive sections, each of which is the equivalent of an ordinary ventral ganglion. Starting with the most posterior of these, a fibre section is seen in which the connective trunks (cn) have merged with each other and in which ventrally on the median line, 2 glia cells are situated which are completely identical with the 2 median cells of the ordinary ventral ganglion. This is followed by a small cavity where the two connectives separate again. Here, each connective trunk contains one glia cell which quite corresponds to the other connective cells of the ventral cord. Further cephalad, the connective trunks again merge three times in the same fashion, to form the 1st, 2nd and 3rd sections of the central fibre mass, each of which is identical to the described 4th except that they gradually become somewhat shorter in longitudinal direction, starting from the most posterior. Between these, the connective trunks separate again, showing the same details seen in the most posterior ganglion section. Caudad from the 1st ganglion section, the connective trunks again separate, thus becoming pharyngeal connectives (scn). Here a lateral bridge consisting of nerve fibres lies between them that forms the anterior surface of the subesophageal ganglion mass; it is the equivalent of the most anterior transverse fibre portion of the subesophageal ganglion mass in the other Hirudinea. Seen ventrally, this transverse fibre portion usually contains 3 glia cells.

Ventrally and laterally, the central fibre mass is covered by the ganglion cell clusters (Fig.24, Nos. 101, 102), while dorsally there are no such clusters. There, one muscle cell is seen on each side along the median line between the 3rd and 4th ganglion complex. Their relationships are identical to those of the above described muscle cells of the ventral cord. Further cephalad, such cells do not occur in the subesophageal ganglion mass.

The ganglion cell clusters (mp, lp), 24 altogether, are arranged according to the 4 sections of the central fibre mass in such a way that the individual ganglion complexes are clearly apparent. Ventrally below each ganglion section is 1 pair of successive median clusters (mp$_1$, mp$_2$, mp$_3$, mp$_4$), of which 8 are therefore present in the entire subesophageal ganglion mass. The clusters of each pair touch those of the adjacent pair, and thus an uninterrupted row of 8 oval median clusters is formed ventrally. The 16 lateral clusters (lp) are also grouped in pairs. On each side of the 4th ganglion complex one pair of clusters (lp$_4$) typical for the ordinary ventral ganglion is accumbent. In the 3rd ganglion complex the lateral clusters (lp$_3$) are slightly broadened laterad, and in the 2nd ganglion complex this characteristic reaches its maximum (lp$_2$). Here the clusters are almost pear-shaped, and their broadened parts project laterally from the subesophageal ganglion mass into the coelom. The lateral clusters (lp$_1$) of the 1st ganglion complex deviate slightly from this type in that they project in the form of 2 elongated ovals on the surface of the corresponding pharyngeal connective. One of them occupies the ventral surface of the first section of the pharyngeal connective, while the other rises on the lateral surface of the same. Thus by and large we find here the same relationships that are characteristic for the Hirudinea type in general.

Corresponding to the 4 ganglion complexes, the nerves of the subesophageal ganglion mass take the following course: On each side, the 4th ganglion complex generates 2 nerves (n$_2$, n$_4$*) which exit from its most anterior part immediately behind the corresponding connective section, i.e. anterior to the lateral ganglia cell clusters. One, the thicker nerve (n$_4$), originates on the margin between the ventral and lateral surface of the central fibre mass; the other nerve, much smaller (n$_4$*), originates slightly higher and and more cephalad. Only one nerve (n$_3$) extends on each side of the 3rd ganglion complex, which, however, is generated through the merger of 2 roots. These roots originate in the anterior part of the corresponding complex, immediately behind the corresponding connective section, i.e. anterior to the lateral clusters of the ganglion complex; their origin is the same as that of the two described nerves with which they are therefore quite identical. Only one nerve (n$_2$) comes from the 2nd ganglion complex: it originates as a thick nerve in the anterior section of its ganglion complex at the margin between the ventral and lateral surface of the central fibre mass. It therefore represents an even higher degree of fusion between two separate nerves. Another such nerve (n_1) also comes from the 1st ganglion complex and runs cephalad between the two lateral clusters (10_1) of the same.

This description shows that the subesophageal ganglion mass of *Acanthobdella* is definitely formed by the merger of 4 ordinary ganglia. KOWALEVSKY (1896, p. 269) indicated this and wrote: "Dans la masse sous-esophagienne on distingue quatres ganglions". In this respect, the characteristics of *Acanthobdella* are the same as those in the other Hirudinea, especially when species such as *Protoclepsis tessellata* or *Herpobdella atomaria* are included in the comparison.

The pharyngeal connectives (scu) are well-developed in *Acanthobdella*. Cephalad 2 nerves come from them, one of which (n*) separates in its middle section, the other (n) in its dorsal section, just ahead of the supraesophageal ganglion mass. At the point of separation of the dorsal nerve, the pharyngeal connectives receive some ganglion nerves which also penetrate its root. This nerve extends cephalad and innervates the 1st pair of eyes of *Acanthobdella* The other pharyngeal connective nerve represents the stomodeal (sympathetic) nerve whose behaviour will be discussed when the intestine is described.

Half-way along the esophagus the pharyngeal connectives merge with the central fibre mass of the supraesophageal ganglion mass (obm; see Fig. 33, No. 1, 2; Fig. 41, No. 101, 102) which surround the esophagus dorsally in the form of a wide arc of fibres. The clusters of the supraesophageal ganglion mass are situated at this arc near where its rising section merges into the horizontal. On each side are 6 ganglion cell clusters. One of them forms an elongated, pear-shaped mass which looks as if it were suspended by its trunk from the lateral surface of the fibre arc, while its broadened part protrudes caudad and laterad. Accumbent to this ganglion cluster are 2 clusters ventrad, 2 clusters dorsad, and 1 cluster cephalad, all of which are oval masses of ganglion cells. One of the two lower clusters extends from the lateral surface to the caudal of the fibre arc, while the other extends to the anterior surface of the same, and the two dorsal clusters have a similar position.

Below these clusters, accumbent to the central fibre mass of the supraesophageal ganglion mass, are 4 glia cells, two of which are below the ventral pair, two below the dorsal pair of ganglion cell clusters. In addition, 2 glia cells, arranged on top of each other, are accumbent to the fibre arc, one pair on the anterior surface, one pair on the posterior surface, where the arc is not covered by the two clusters. Thus on each side of the central fibre mass of the supraesophageal ganglion mass, 8 glia cells are situated whose appearance is identical to that of the connective or median cells. However, their number can vary; the author occasionally noted 6, sometimes 7 cells.

In *Acanthobdella* as well as in the other Hirudinea, no nerve cells come directly from the supraesophageal ganglion mass.

The above indicates that the supraesophageal ganglion mass of *Acanthobdella* is formed according to the general Hirudinea type. Especially obvious is the similarity with the characteristics illustrated in F. LEYDIG (1864) for *Haemopis vorax* Brandt, and which the author has discussed in detail earlier (LIVANOW, 1904, 2). The arrangement of the ganglion cell clusters in the supraesophageal ganglion mass of *Acanthobdella* can thus be regarded as rather primitive, closely resembling the arrangement that was ancestral to the further development of this organ in the Hirudinea.

The 5th head somite (5) of Acanthobdella is innervated exclusively by the ordinary ventral ganglion (gn_5) which it contains, and thus the structure of the corresponding neurosomite is quite typical (Fig. 41, No. 101).

By and large, the musculature of the body wall (rm, dm, lm) has the usual characteristics, except that it contains all the peculiarities in which the head somite differs from the other somites of the body. As mentioned above, the 5th head somite is ventrally flattened. This is caused by the fact that the ventral sector of the body wall in this somite is gradually shortened. In the 4th annulus of this somite it can be seen that the longitudinal muscle fibres of the longitudinal muscle strands, which extend ventrally along the lateral line of the body, are condensed. These muscle fibres are arranged closer together and form several layers above each other. This process takes place mainly in those longitudinal muscle strands that extend directly below the lateral line and mediad from the intermediate line. In the 3rd annulus this phenomenon is already more pronounced, so that in the 2nd annulus the ventral surface looks considerably flattened, while the dorsal surface remains arched as before (Fig. 33, No. 3). As a result, the lateral nerve with the corresponding part of the integument has shifted ventrad from its former position, and the space between the dorsal and ventral muscles has turned ventrad. On the other hand, the muscle strands situated immediately dorsad of the lateral line have separated slightly, thus somewhat enlarging the lateral surface of the body. This characteristic already reflects the secondary adaptation to the special function of the head end as attachment organ. In this connection, A. KOWALEVSKY (1896, p. 264) noted: " Elles (the Acanthobdellis) s'attachent avec la bout antérieur aux parois du corps et les soies leur aident à se fixer". To enable it to attach itself to the host by means of the chaetae, the worm requires these barbs at the ventral side of its head end, and this is achieved mainly by the shortening and flattening of the ventral surface of the head.

The chaetae (bs) which are encountered for the first time in the 5th head somite, are situated in its 2nd annulus (Fig. 33, No. 1, 3; Fig. 35, No. 17 bsz_5). One pair (bs*) occupies the space between the dorsal and ventral longitudinal muscle strands, while the other (bs) is situated in the space between the ventral longitudinal muscle strands on the ventral intermediate line of the body (Fig. 33, No. 3); thus the two pairs of chaetae are facing ventrad.

In connection with the chaetae of *Acanthobdella*, GRUBE (1851) wrote: "The tip of the barbs has a simple curvature; their size is so insignificant that I failed to see them during my first examination of a specimen in spite of their dark brown colour, and their shape was recognizable with complete certainty only at a magnification of 60x". KESSLER (1868) wrote: "The barbs of each individual pair seem to grow together at their base. They have a very elongated hook, but in their dormant state they only extend above the skin by their curved heads. Apparently these barbs form an apparatus with which the worm can tightly cling to the skin of the host". KOWALEVSKY (1896, p. 265) wrote: "Les auteurs qui ont décrit l'*Acanthobdella* ont donné une description assez exacte de leurs soies du bout antérieur du corps, mais personne n'a mentionné l'existence des petites soies de remplacement qu'on trouve à la base des grandes soies, et qui servent sans doute à remplacer les soies usées oy perdue: souvent ces soies s'accroissent et deviennet aussi longues que les autres".

As mentioned, 1 pair of chaetae (bs) is situated in the ventral intermediate line, the other (bs*) in the lateral line (Fig. 33, No. 3). In these areas, the skin epithelium of the 2nd annulus of the 5th head somite forms 2 pairs of inward proliferations, the chaetal sacs (bsc), where the two inward proliferations of each pair are almost directly adjacent to each other and practically form one whole (Fig. 33, No. 3; Fig. 35, No. 17). Each pair pushes the longitudinal muscle strands apart and penetrates the inner body mesenchyme, turning slightly caudad in the process. The chaetal sacs are club-shaped, and their broadened section may more or less project into the coelom, while that of the ventral pair is directed laterad, that of the lateral pair mediad. The free coelom ends of the chaetal sacs are naturally covered by coelothelium (Fig. 38, No. 56).

Since the chaetal sacs are a direct continuation of the skin epithelium, their cell elements, especially in the collar-shaped initial sections of the inward proliferation, consist of typical epithelial cells, although their shape is variously altered, and the cell margins are poorly defined. The further into the inner body mesenchyme they extend, i.e. toward the broadened end of the chaetal sacs, the more these cells are changed (Fig. 38, No. 54-56, 58). The nuclei become larger and contain more chromatin; at last they are vesicular or ovoid and endowed with many chromatin globules; they have a diameter of about 20-30 µ. Accordingly the cell body itself is also very considerably enlarged, although the margins remain poorly defined as before. In addition to such cells (bsz), ordinary small cells (bsz*) occur as well, which so to speak form the reserve material for the development of new large cells.

In some cells of medium size, a small cuticular formation, an insignificant barb (Fig. 38, No. 54 bs) can be observed. As the formative cell grows, this first rudimentary chaeta becomes enlarged as well, and the small curved chaeta pushes through between the adjacent cells. Around the thus developed chaeta, the accumbent cells apparently do not secrete another sheath or membrane. The chaetae are longitudinally striated, and they look as if they were composed of fine cuticular fibres cemented to each other. The striation is particularly evident at the inner end of the chaeta (Fig. 38, No. 55) that borders on the plasm of the formative cell. In the protoplasm of even this cell, which here is very light and transparent, a cone of protoplasm threads can be observed that looks like a continuation of the striation of the chaetal end toward the nucleus. The larger the formative cell becomes, the more the hook of the barb becomes elongated, and its curved tip becomes quite homogeneous and light in colour. This latter process seems to be caused by a thickening of the substance at the tip of the chaeta. If the chaetae are of medium size, the nucleus of the formative cell usually lies somewhat laterad. However, when the chaetae are completely developed and protruding from the integument, the nucleus is far to the side (Fig. 38, No. 56), and the associated cell plasm covers only the inner end of the chaeta as the cap of a very thin sheath. At that time, the chaeta is homogeneous, and only at its inner end can a trace of striation still be noted. Because of the described thickening, the chaeta has now become spindle-shaped, with a curved tip (Fig. 33, No. 3), and the broadening in the middle, which is closer to the free end of the chaeta, is sometimes very clearly defined. In this last stage of its development the chaeta can apparently be pulled from its sheath quite easily, which may in fact happen quite frequently in live worms.

As the above description shows, the development and structure of the chaetae of *Acanthobdella* definitely are of the same type as those found in many Oligochaeta, and especially in *Haplotaxis gordioides*. In this species, some of the chaetae have an inner end that is completely straight as in *Acanthobdella*.

In *Acanthobdella*, each chaetal sac (bsz) contains only a single fully-grown chaeta (bs) which "predominates" in the sac (Fig. 38, No. 57). It is usually noticeable from the outside as a small, curved barb (Fig. 33, No. 1, 3; Fig. 3, No. 19). Occasionally a second chaeta can be observed in addition, which is always in the same annulus and somewhat smaller than the first. This is the substitute chaeta, i.e. the chaeta formed in the same chaetal sac, which takes over the function of the first chaeta if it should fail. In the distal section of the chaetal sacs only the single main chaeta and occasionally the oldest substitute chaeta can be found; the cells of the sac are closely accumbent to the chaetae and form a kind of epithelial sheath around them (Fig. 38, No. 58). On the other hand, in the upper broadened part of the chaetal sac that projects into the coelom, one usually finds not only the proximal ends of the described chaetae, but also a very small barb (bs*) of the 2nd substitute chaeta which plays the same role for the 1st substitute chaeta as it does for the main chaeta. Occasionally a 3rd substitute chaeta is present which is situated in the innermost end of the chaeta; it is a hardly noticeable, insignificant rudiment, as described above

(Fig. 38, No. 54). Thus occasionally all stages of chaetal development can be studied in the same epithelial proliferation. In this respect, the characteristics of *Acanthobdella* are extremely similar to those in many Oligochaeta, especially in Terricola.

A well-developed, specialized muscle apparatus serves to move the chaetae (Fig. 35, No. 19).

Three muscle cells extend cephalad to the proximal section of the ventral pair of chaetae. 2 of them (mz_2) come from the 4th annulus (IV) of the 5th head somite, between the fibres of the 2nd ventral muscle strand (counted from the lateral line of the body), then gradually curve into the inner body mesenchyme and finally attach themselves to the sector of the chaetal sacs that projects into the coelom. The 3rd muscle cell (mz_1) also attaches itself there with one end, while the other end inserts on the ventral intermediate line at the integument of the 3rd annulus (III) of the described head somite. In the plane of the chaetae 3 or 4 similar chaetae can be observed which only differ from those just described in that their distal ends are attached at the integument directly around the chaetal sacs. In addition, from the ventral pair of chaetae one, sometimes two pairs of muscle cells (mz) extend cephalad which are characterized by their thickness and pronounced ramification at their ends. These cells attach themselves on one side at the inner section of the chaetal sacs, on the other side on the ventral intermediate line, at the integument of the 4th or 3rd ring of the 4th head somite. As can be seen, the muscle apparatus of the chaetae consists mainly of fibres that insert caudad, cephalad, and in the plane of the chaetal sacs on the ventral intermediate line of the integument; only 2 muscle cells extend to the lateral line of the body.

This muscle complex which alone enables the ventral pair of chaetae to perform a variety of movements, is joined by another muscle cell which is none other than a muscle fibre from the diagonal musculature, namely that of the 3rd annulus in the 5th head somite (Fig. 35, No. 18). It is a strongly developed muscle cell with greatly ramified ends, one of which inserts at the ventral, distal section of the chaetal sacs, the other at the integument above the dorsal paramarginal longitudinal muscle strand in the 3rd annulus of the 5th head somite.

Somewhat less developed is the muscle apparatus of the lateral pair of chaetae, which can be explained by the position of the chaetae near the transition between the ventral and the dorsal body surface, and thus by its lesser role in the attachment function of which the anterior end of *Acanthobdella* has. Distally this pair of chaetae is joined only by a single muscle cell whose proximal end is attached at the inner section of the chaetal sacs, while the distal end attaches itself to the integument on the dorsal intermediate line in the 3rd annulus of the 5th head somite. This cell apparently corresponds to the muscle cells of the ventral pair of chaetae that run to the lateral line of the body. In the plane of the chaetae 2 or 3 muscle cells are situated which insert on one side at the proximal end of the chaetal sacs, on the other side at the integument near their distal sections. In this they are fully identical with the ventral pair of chaetae. As in those, a thick muscle cell extends cephalad from the proximal section of the lateral pair of chaetal sacs, and this cell then attaches itself at the integument on the ventral intermediate line in the 4th annulus of the 4th head somite. It should also be noted that a well-developed diagonal muscle cell is present here (Fig. 35, No. 18; Fig. 38, No. 58 mf) whose one end inserts at the integument of the 2nd annulus of the 5th head somite on the dorsal paramarginal line of the body and whose other end is fixed in the distal section of the lateral pair of chaetal sacs. Thus by and large the muscle apparatus in both pairs of chaetae is very similar in type.

All described muscle cells have the same structure as the lateral, dorsoventral or annular muscle cells. Their ends are mostly ramified, and the contractile-fibrillar layer is absent over a more or less considerable part of the periphery of the nucleate cell sector. The terminal rami (mf*) of the muscles are directly accumbent to the chaetal sacs without showing any special type of adhesion (Fig. 38, No. 57).

In some cases the author was able to detect the presence of a special nervous apparatus on the chaetal sacs (Fig. 38, No. 58). It is a unipolar ganglion cell (gnz) which laterally to the epithelial proliferation is accumbent to one or the other pair of chaetae. Its process divides into a few branches which extend toward the respective pair of chaetae. In other cases such a ganglion cell seems to be absent, although the author thinks it much more probable that it is present, but that it is so closely accumbent to the cells of the epithelial proliferation of the chaetal sacs that it is impossible to differentiate them from the cells of the latter. The processes of the ganglion cells could also very easily escape detection in the surrounding tissue.

At the end of our description of the body wall of the 5th somite of the head region of *Acanthobdella*, we wish to look at the associated sensory organs (sk). By and large their distribution (Fig. 33, No. 3; Fig. 41, No. 101) seems to be quite similar to that in the ordinary somites of the mid body, but their development is only dorsally of the same degree. The groups of sensory buds that are usually present in the 2nd somite annulus on the paramedian (pmd_1) and intermediate (int_1) line of the body, are particularly well-developed here, and their cells project through the longitudinal muscle layer into the inner body mesenchyme. Between those mentioned, 2 or 3 additional sensory buds are present, but their development seems to be more or less retarded.

The cells of the sensory buds on the lateral line of the body distally surround the chaetal sacs of the lateral pair, and a varying number of their cells seems to be entering the space between the latter (Fig. 33, No. 3). The proximal sector of these sensory buds enters the inner body mesenchyme where it lies below the longitudinal musculature dorsally and laterally of the chaetae (bs*). It ends in a peculiarly differentiated structure that represents a special sensory organ, namely the eye (au_3). The latter is situated in the anterior section of the 2nd annulus of the 5th head somite, dorsally of the lateral line of the body and directly anterior to the lateral pair of chaetal sacs (Fig. 33, No. 1, 3; Fig. 35, No. 17).

As mentioned above, well-developed retinal cells (rz) can quite often be observed in the proximal sector of the lateral sensory buds in the mid trunk somite of *Acanthobdella* (Fig. 36, No. 25). The end sector of the lateral group of sensory buds in the 5th head somite is also formed by 4-6 such cells with a well-developed light-refracting inner body. Here the retinal cells form an oval body (au_3) whose longitudinal axis has a dorsoventral direction (Fig. 33, No. 3). The margins of the individual cells (rz) which are closely accumbent to each other (Fig. 38, No. 59, 60)[1] can always be observed in this body, although on the whole they are quite poorly defined. Seen from the front and the sides, the retinal cells are covered by a layer of oval pigment cells (pz). They form a pigment cup which remains open caudad and ventrad and which – together with the retinal cells with which it is filled – forms the eye. In respect to the structure of the eye of *Acanthobdella* in general, A. KOWALEVSKY (1896, p. 226) commented as follows: "Les cellules pigmentaires qui forment la couche noire de l'oeil ne contient pas des granules adipeux; elles se décolorent aussi par l'alcool et le sublimé". However, the author has observed the opposite, namely that the 8-10 cells which form the pigment cup are typical pigment-fat cells of the mesenchyme with a more or less significant amount of fat droplets in the protoplasm. However, one of their peculiarities is that they do not contain pigment as usual, over the entire periphery of the cell, but only in the cell portion that faces the retinal cells. In specimens fixed in osmic acid (Fig. 38, No. 60), a seam about 10 μ wide can be observed here that is filled with brownish-black pigment granules. The latter reach their maximum size at the cell's periphery, while inwardly in the the cell plasm they appear only as finest dust particles until they disappear completely. In specimens fixed with sublimate or alcohol, one sees instead of this pigment seam a very transparent, finely radially striated protoplasm layer (Fig. 38, No. 50). This means that the pigment granules are embedded in these fine plasm threads of the peripheral cell layer which cannot be observed as long as the pigment is still active.

---

[1] Fig. 59 and 60 actually show the 1st pair of eyes. However, since all pairs of eyes have exactly the same histological structure in *Acanthobdella*, these illustrations can also serve to explain the present case.

The above leaves no doubt that the eyes of *Acanthobdella* are derived from ordinary sensory buds from which they have evolved by differentiation of a certain number of retinal cells and the formation of a layer of pigment-fat cells surrounding the latter. To complete this description, it should be noted here that the processes of the retinal cells which form the eye nerve extend ventrad and toward the lateral line and – together with the other sensory fibres of the lateral sensory buds – enter the sensitive nerve of the 5th head somite which passes in very close proximity.

The facts just described are thus in complete agreement with the author's earlier observations (LIVANOW, 1904, 2) and leave no doubt that the eyes of *Acanthobdella* are fully homologous to those of the other Hirudinea.

As far as the structure of its body wall is concerned, the 4th somite (4) of the head region of *Acanthobdella* has more or less the same relationships as those described for the 5th head somite. Its sensory buds and eyes ((au_2) as well as its chaetae and their structure, position and arrangement are quite identical with those of the corresponding organs in the 5th head somite (Fig. 33, No. 1; Fig. 35, No. 17; Fig. 41, No. 101). Insignificant differences are found in the muscle apparatus of the chaetae. Thus 2 muscle cells that run caudad and laterad from the ventral pair of chaetae are attached to the integument not ventrad of the lateral line, but slightly dorsad of the latter. Always extending cephalad from the same pair of chaetae are 2 thick muscle cells which as usual insert in the posterior section of the previous, i.e. 3rd head somite on the ventral intermediate line. The muscle apparatus of the lateral pair of chaetae of the 4th head somite contains no muscle cell running caudad and toward the dorsal intermediate line, but instead a muscle cell that attaches itself – as in the first pair of chaetae – with one end to the proximal sector of the chaetal sacs, with the other end to the integument of the posterior annulus of the 4th head somite on the ventral intermediate line. Cephalad from this pair of chaetae run 2 muscle cells showing relationships similar to those described for the ventral pair.

However, all these deviations are of subordinate importance, and the basic type of the muscle apparatus is really the same for all pairs of chaetae in spite of a few specific modifications in some cases.

Another insignificant difference from the 5th head somite is the further shortening of the ventral sector of the body wall in the 4th head somite and thus also the further concentration of longitudinal muscle fibres which are arranged even more compact and closer together, especially mediad from the ventral intermediate line. In connection with this, the spaces between the longitudinal muscles on the intermediate and lateral line of the body have shifted more toward the ventral side, while the dorsal surface of the body wall has somewhat enlarged lateral sectors. The described characteristics are also the result of a general reduction of the dimensions of the somite and its approximation to the anterior end of the body.

The 4th head somite is innervated exclusively by 2 pairs of nerves (n_4, n_4*) of the 4th ganglion complex of the subesophageal ganglion mass (Fig. 41, No. 101).

The thick posterior nerve (n_4) is a composite formation and is the equivalent of the posterior motor nerve and the middle sensitive nerve of the ordinary somite of the mid body which are united in a single trunk. This is proven by the peripheral characteristic of the described nerve. After it has reached the ventral paramedian longitudinal muscle strand in typical fashion, it divides into 2 branches, the smaller of which continues in the 3rd somite annulus where it forms a typical posterior ring nerve, while the larger enters the 2nd somite annulus and shows the characteristics typical for the sensitive nerve of the somite. However, sometimes the development of the two branches of this nerve (n_4) is not as pronounced (Fig. 41, No. 101), in that the nerve first generates a small branch (hnz_4) that runs from the ventral paramedian longitudinal muscle strand to the 4th somite annulus. This small branch has all the characteristics of the branch associated with the posterior ring nerve. Only then, ahead of the ventral intermediate longitudinal muscle strand, the latter itself separates and divides into 2 branches, the smaller of which continues into the 3rd somite annulus where it displays the characteristics of a typical posterior ring nerve of the somite (rn_2), while the other runs into the 2nd somite annulus behind the chaetal sacs where it forms a typical sensitive nerve (sn_1) of the somite.

The anterior nerve (n_4) of the 4th complex of the subesophageal ganglion mass is of insignificant thickness; it enters the 1st annulus of the 4th head somite and represents an ordinary anterior ring nerve of the somite ($rn_{4(1)}$).

This shows that the neurosomite of the 4th somite of the head region has a more or less typical structure and that the 4th ganglion complex of the subesophageal ganglion mass constitutes the central section of the same.

The innervation area of the only pair of nerves (n_3) extending from the 3rd ganglion complex of the subesophageal ganglion mass has a similarly rigid delineation, in that it expands to the 3rd head somite (3) only (Fig. 41, No. 101).

Upon its entry into the body wall this nerve divides into two main branches. The characteristics of one quite resemble those of the posterior nerve of the 4th head somite, while the other (smaller) corresponds to the anterior nerve of the latter. Taking into account that the described nerve originates through the fusion of 2 roots, it can be concluded that the two independent nerves of the 4th head somite form a single nerve in the 3rd somite only over a short distance after they leave the subesophageal ganglion mass.

In detail, the described nerve has the following characteristics: Its larger branch penetrates the 1st longitudinal muscle strand (counting from the median line of the body) where it divides into 3 branches. The smaller of these (hnz_3) enters the posterior section of the 2nd annulus of the 3rd head somite; in terms of its relationships it is none other than the ordinary branch of the posterior ring nerve for the posterior annulus of the somite. However, this nerve branch usually does not reach the lateral line in the 3rd head somite, since it gradually becomes thinner until it disappears behind the ventral intermediate longitudinal muscle strand. Occasionally it remains completely undeveloped. One ($rn_{3(2)}$) of the two remaining branches runs in the anterior section of the 2nd annulus of the 3rd head somite and represents the typical posterior ring nerve of the latter; the other (most important) branch (sn_3) enters the posterior section of the 1st annulus of the same somite where it forms the completely characteristic sensitive nerve of the same.

The smaller nerve ($rn_{3(1)}$), which was formed by the 1st ramification of the described nerve of the subesophageal ganglion mass, begins its course in the anterior section of the 1st annulus of the 3rd head somite and represents the characteristic anterior ring nerve of the latter. However, it is distinguished from the corresponding nerves of all following somites of the body by the absence of the annular muscle fibre that otherwise accompanies this nerve.

The described facts indicate that the neurosomite of the 3rd head somite, similarly to the 4th and 5th somites of the head region, has a generally typical development and originates centrally in the 3rd ganglion complex that belongs to the subesophageal ganglion mass.

We will now look at the body wall of the 3rd head somite. It should be noted that the shortening of its ventral surface is even more pronounced than that of the 4th head somite (Fig. 33, No. 2). In the anterior section of the described somite, all ventral longitudinal muscle fibres are concentrated in only 3 muscle strands. We first encounter a muscle strand (pmd_1), mediad of the intermediate line of the body, which is formed mainly by the elements of the paramedian muscle strands and constitutes the direct continuation of the latter. The other 2 muscle strands are situated between the intermediate and lateral lines of the body and prove to be the continuation of the intermediate (int_1) or paramarginal (pmr_1) muscle strand, respectively.

Another change in the musculature of the 3rd head somite is that the characteristic Oligochaeta dorsal muscle fibre has been replaced in this somite by the type of ordinary muscle fibre that is characteristic for the Hirudinea. It is an insignificant muscle cell whose ends are not ramified, whose nucleus is without a contractile-fibrillar layer over almost half of its periphery, and which lies in the most anterior part of the somite, directly anterior to the marginal furrow between it and the previous somite.

The 3rd head somite is already lacking the characteristic giant cells of the diagonal musculature whose fibres, entering from the 4th head somite, gradually disappear.

The sensory buds of the 3rd somite of the head region (Fig. 41, No. 101) which are arranged in the posterior portion of the 1st annulus of the latter along the same lines of the body as in all following somites, are well-developed not only dorsally but also ventrally. They enter the longitudinal musculature and project into the inner body mesenchyme. The sensory buds which lie on the lateral line form a well-developed sensillum: in their proximal sections are 3-4 retinal cells.

The latter are covered cephalad and dorsad by ordinary pigment-fat cells. If the pigment were concentrated on the side facing the retinal cells, we could observe a typical eye that is developed only slighly less than in the 4th and 5th head somite.

In addition, the 3rd somite of the head region has true Hirudinea eyes, representing the 1st pair of eyes (au_1) of *Acanthobdella* (Fig. 33, No. 1; Fig. 35, No. 17; Fig. 41, No. 101). They lie on both sides of the dorsal median line in the inner body mesenchyme, directly below the longitudinal muscle strands (Table 35, No. 17; Table 38, No. 59). Each eye is very well-developed and consists of 8-10 oval retinal cells (rz) which are surrounded caudad, dorsad and laterad by a layer of pigment-fat cells (Fig. 38, No. 59, 60). In terms of position and structure, the pigment layer of the latter seems to be quite identical to that of the above described eyes in the 4th and 5th head somites. By and large, the eyes of the described somite differ from those of the following somites only in that (apart from their better development) they are innervated by the pharyngeal connective nerve and seem to lack any connection with sensory buds. Only occasionally a direct connection is found between the eye and the proximal portion of the paramedian dorsal sensory bud, which is usually greatly masked by the fact that the elements of the pigment cup are inserted between the retinal cells on the one side and the sensory cells of the proximal portion of the sensory buds on the other side. Thus it appears that the eyes of the 3rd head somite are homologous to those in all other somites of *Acanthobdella*, and that they have also developed through the differentiation of sensory buds on the dorsal paramedian line of the body. As will be discussed below, this is confirmed by the fact that a well-developed sensillum is present on the same line of the body in the previous (2nd) head somite. As far as the innervation of the eyes of the 3rd head somite by the dorsal pharyngeal connective nerve is concerned, this is easily explained by the shift of the relevant nerve fibres from one bundle to another, closer to their place of destination (this frequently happens elsewhere).

As far as the chaetae of the 3rd head somite are concerned, it should be noted that the development of their muscle apparatus seems to be generally the same as in the 4th and 5th head somites.

Insignificant deviations exist only in that the ventral pair of chaetal sacs has only 1 instead of 2 muscle cells extending caudad and laterad, and that of the 2 cells running cephalad in the 4th somite, one is not ventrally attached to the integument, but at the dorsal paramarginal line of the body. Contrary to the characteristics described for the 2 following head somites, the muscle apparatus of the lateral pair of chaetae is formed as that of the ventral pair, by receiving the same muscle cells in the same position, namely: 2 cells extending caudad, 3 situated in the plane of the chaetal sacs, 2 extending cephalad, and 1 diagonal muscle cell. This fact confirms the author's assumption that the type of the muscle apparatus is the same for all pairs of chaetae, and that only insignificant differences exist from one pair to another.

At the end of this description it should be emphasized that because the 3rd head somite has been reduced to 2 annuli, its chaetal sacs, which originate in the posterior portion of the 1st ring and usually assume a posterior direction while entering the inner body mesenchyme, project with their proximal ends as far as the 1st annulus of the 4th head somite.

The same is expressed to an even greater degree in the position of the proximal portions of the chaetal sacs in the 2nd and 1st head somites.

As indicated during the discussion of the external morphology of the head of *Acanthobdella*, the annulus forming the 1st head somite lies all ventrally (Fig. 35, No. 17), and therefore the ventral portion of the following annulus that constitutes the 2nd somite of the head region seems to be greatly shifted caudad in comparison with the dorsal portion of the same. The vertical plane that ventrally passes the 2nd head somite bisects dorsally the most posterior annulus of the 3rd somite of the head region. Similarly, the ventral, i.e. post-oral portion of the 1st head somite lies in the vertical plane which dorsally meets the most anterior annulus of the 3rd somite.

Because of these interrelationships of the anterior head somites, the chaetal sacs of the 1st and 2nd somites, after they have entered the inner body mesenchyme where they turn slightly caudad as usual, project with their proximal ends into the coelom of the 3rd head somite. Thus it happens that in the coelom, laterally of the dorsal portion of the pharyngeal connectives and supraesophageal ganglion mass (obm), are encountered first the proximal ends of the chaetal sacs of the ventral pair belonging to the 1st head somite (bsz_1) and further laterad the same sections of the corresponding chaetal sacs of the 2nd head somite (bsz_2; see Fig. 33, No. 2). In the anterior portion of the 3rd somite of the head region, the proximal ends of the corresponding lateral chaetal sacs are situated above the middle portions of the above named chaetae.

Since the chaetal sacs and their chaetae do not differ in any way from those of the 3 posterior head somites, we will now describe their muscle apparatus. Caudad from the proximal end of the ventral pair of chaetal sacs of the 2nd head somite a muscle cell extends as usual, which inserts on the dorsal paramarginal line of the body in the integument of the posterior portion of the 3rd somite. Another such cell extends to the ventral intermediate line into the posterior portion of the 2nd head somite. In addition there is a diagonal muscle cell which attaches itself with one end to the distal portion of the chaetal sacs and with the other end to the posterior portion of the 3rd head somite on the dorsal paramarginal line. In addition to these ordinary cells of the muscle apparatus for the chaetae of *Acanthobdella*, a thick muscle cell with greatly ramified ends originates in the proximal portion of the mentioned pair of chaetal sacs, which extends caudad and attaches itself to the integument of the posterior portion of the 3rd head somite on the dorsal paramedian line of the body. Such cells are absent in the muscle apparatus of the above discussed somites. The muscle cells situated in the plane of the given pair of chaetae and those extending from that pair cephalad and dorsad show the same development as in the following (3rd) somite, but it should be noted that the cell extending cephalad and dorsad is attached to the integument in the mid portion of the last mentioned somite.

The muscle apparatus of the lateral pair of chaetae of the 2nd head somite is identical to that described for the lateral pair of chaetae of the 4th somite. The only difference is that it contains a muscle cell that extends caudad and laterad from the proximal portion of the chaetal sacs. It attaches to the integument in the anterior portion of the 3rd head somite on the dorsal paramarginal line.

Thus we see that the muscle apparatus of the chaetae of the 2nd head somite is of the same structural type as that in the above described 3 following somites of the head region. The only peculiarity (caused by the interrelationships of the anterior head somites) is that the dorsal points of attachments of the muscle cells have shifted caudad where they are all situated, as discussed above, in the 3rd head somite. In addition, the cells of the annular musculature form a closer relationship with the chaetal sacs in the 3rd head somite, which can probably be regarded as the result of the considerable progressive cephalad reduction, especially of the ventral portions of the head somites. Thus between the ventral pairs of chaetae a muscle cell is situated whose one end inserts at the distal portion of the right pair of these chaetal sacs, while the other inserts in the same place of the left pair, and another similar cell connects the distal portions of the ventral and lateral pairs of chaetal sacs on one and the same side of the body. It should also be mentioned that the proximal portions of these chaetal sacs are connected with each other on each side by a muscle cell.

The most complicated and the most deviating from the general type is the muscle apparatus of the chaetae of the first head somite of *Acanthobdella*, which is naturally caused by the position of the somite, which is situated quite ventrally at the head and at the same time forms the anterior end of the body, but also by the fcat that its dimensions are greatly reduced in comparison with the following head somites. A certain influence must also be ascribed to the circumstance that the centre of the above somite lies in the oral opening.

We will now examine this muscle apparatus somewhat closer.

As in all following head somites, 1 or 2 muscle cells extend caudad from the proximal portion of the ventral pair of chaetal sacs; they run slightly laterad and attach themselves to the integument of the posterior portion of the 3rd head somite on the median side of the dorsal paramarginal line of the body. Another cell extends ventrad and attaches itself to the integument of the 1st head somite, slightly mediad of the ventral intermediate line, near its posterior margin. There is also a well-developed muscle cell with greatly ramified ends, of the type we have found only in the ventral pair of chaetae of the 2nd head somite; its one end inserts at the proximal portion of the above mentioned pair of chaetal sacs, while its other end inserts at the posterior annulus of the 3rd head somite on the dorsal paramedian line of the body. The diagonal muscle cell which usually extends from the distal portion of the chaetal sacs caudad and to the dorsal paramarginal line, here runs to the same area of the integument, and cephalad to the anterior portion of the 3rd head somite, while the clusters of the secretory ducts of the giant glands project between this cell and the corresponding chaetal sacs. This is the only muscle cell belonging to the mentioned pair of chaetal sacs and running in dorsal direction whose dorsal point of attachment has only undergone a relatively slight shift caudad. In all others, this phenomenon which, as mentioned, is caused by the displacement of the 1st head somite to the ventral side, is far more pronounced. For the same reason, one of the two cells running cephalad from the proximal portion of the chaetal sacs (the well-developed muscle cell that is directed dorsally) is attached to the anterior annulus of the 3rd head somite. In contrast to all following somites of the head region, this cell crosses over to the opposite body side, having crossed the corresponding cell of the other side on the median line of the body, and it inserts at the integument in the area if the dorsal paramedian line. The other of the two above named muscle cells runs as usual to the most anterior oral margin of the 1st head somite where it attaches itself to the integument on the ventral intermediate line of the body. In the plane of the ventral pair of chaetae of the 1st head somite, as in all described somites of the head region, 3 muscle cells run to the integument from the proximal ends of the chaetal sacs near the ventral portions of the latter; however, some of these attach themselves to the intestine in the vicinity of the oral opening.

This description allows the conclusion that the muscle apparatus of the ventral pair of chaetae of the 1st head somite differs very little from that of the ventral pair of chaetae of the 2nd somite, and that the latter forms a connecting link between the just described and the muscle apparatus of the chaetal sacs in the following head somites. The similarity of the apparatuses of the two anterior head somites is also expressed by the fact that some of the annular muscle cells of the 1st head somite are closely related to the chaetal sacs, as are those of the 2nd somite. 1 or 2 such cells connect the distal portions of the ventral pairs of chaetal sacs on both sides with each other, and a similar muscle cell connects the distal portions of the two pairs of chaetal sacs on the same side. Finally, cephalad of the oral opening runs a muscle cell which attaches itself with one end to the distal portion of the right lateral pair of chaetal sacs, with the other end to the same point of the corresponding left pair.

From the proximal portion of the lateral pair of chaetal sacs of the 1st head somite 2 muscle cells extend caudad, one of which attaches itself as usual to the integument of the posterior portion of its somite on the ventral intermediate line of the body. The other cell reaches the dorsal paramedian line of the posterior annulus of the 3rd somite, similar to the muscle apparatuses of the ventral pairs of chaetae of the 2nd and 3rd head somites, but it crosses the median line and thus enters the opposite half of the body. The mentioned pair of chaetae is lacking the muscle cell that extends caudad and laterad. As in all other head somites, a diagonal muscle cell extends from the distal portion of these chaetal sacs and inserts at the integument of the anterior annulus of the 3rd head somite dorsally of the lateral line of the body. In the plane of the chaetal sacs are 2 or 3 muscle cells whose ordinary relationships are obscured only by the fact that the ventral attachment points of some have been shifted towards the oral opening. Of the two muscle cells extending cephalad from the chaetal sacs, only one is retained here which runs dorsad. As in the ventral pair of chaetae, it attaches itself to the anterior annulus of the 3rd head somite on the paramedian line, after entering the integument of the opposite body half. Finally, a particularly thick muscle cell should be mentioned that is closely related to the described muscle apparatus. This cell curves mediad around the lateral pair of chaetal sacs and inserts its one end dorsally of the lateral line of the body in the 2nd head somite, and the other end in the 1st somite near the same point (Fig. 38, No. 61 mz).

This description shows that, although there is a certain difference between this or that ventral pair, largely the absence of certain muscle cells in the muscle apparatus of the lateral pair of chaetae of the 1st head somite, the general structural type of these two muscle apparatuses is the same, and the peculiarities which we have shown to exist in the ventral pair of chaetae also clearly occur in the lateral pair, where they are sometimes even more pronounced.

If we compare the muscle apparatus of the chaetal sacs of the lateral pair of the 1st head somite with the corresponding structures of the 5th somite, quite a considerable difference can be found between them. However, since the somites between them represent a well-defined series of transitional stages, there can be no doubt that all chaetal sacs of *Acanthobdella* and the associated muscle apparatuses definitely belong to the same type and are completely homologous to each other. The peculiarities which are found in the individual somites are quite insignificant and the result of secondary adaptation to the interrelationships that exist between the different head somites.

For this reason the author feels that it is possible to call the chaetal complex a feature which is generally characteristic for the somite of the head region of *Acanthobdella*.

As far as the sensory organs of the 1st and 2nd head somite are concerned, the conclusion is that the entire ventral body surface of the latter is covered by a considerable number of sensory buds whose cells project through the longitudinal muscle layer as far as the inner mesenchyme of the body. It is impossible to determine the exact number and arrangement of the sensory buds, since the somite surface they occupy is greatly reduced, while the buds themselves are distributed very unevenly and without any recognizable regularity.

The situation is different in the case of the lateral and dorsal sensory organs of the two described somites (Fig. 41, No. 101).

On the lateral line of the body, the 2nd head somite has a well-developed sensillum that lies cephalad of the corresponding pair of chaetae.

The sensillum usually contains 2 or 3 retinal cells. At the same point in the 1st somite of the head region we alrady find an ordinary group of sensory buds as it occurs in the mid-trunk somite. Thus a whole row of sensilla of the lateral line is found at the head end of *Acanthobdella* This organ is only slightly more developed in the 2nd head somite than in the 1st head somite or in the ordinary somites of the mid body. In the corresponding sensilla of the 3rd head somite the number of retinal cells is even higher, and this sensillum therefore constitutes a direct transition to the eye of the 4th head somite. The eye itself is really nothing but the group of retinal cells of a certain sensillum that is equipped with with a special sheath of pigment-fat cells. This row is highly informative and again confirms the opinion of C. WHITMAN that the eye of Hirudinea is only a product of the complication and further differentiation of an ordinary sensillum of the body.

In contrast to the ventral portions, the dorsal portions of the 1st and 2nd head somite contain well-differentiated and regularly arranged sensory buds (Fig. 38, No. 61 sk, sk*; Fig. 41, No. 101). In the 2nd head somite they are on the intermediate line of the body as in all other somites. On the paramedian line is a sensillum that contains 2 or 3 retinal cells and, as mentioned, constitutes the transition between an ordinary group of sensory buds of this line and the eye. In the 1st head somite the group of sensory buds on the paramedian line is already without retinal cells and is identical to the other dorsal group of sensory buds of this somite which lie between it and the lateral buds.

The sensory cells of the mentioned sensory organs (sk, sk*) project very deeply into the inner body mesenchyme, where a varied collection of elements of different origins is found, since the proximal portions of all these sensory buds and sensilla of the 1st and 2nd head somite almost touch each other in the mesenchyme, a fact caused by the reduced size of the somite in proportion to its approximation to the anterior end.

We can therefore state that the structure and distribution of the sensory organs of the 2nd head somite are of the same type as those in the other head somites, and that this characteristic is poorly defined only on the ventral side. The same applies to the 1st somite of the head region.

Except for those described above, the head end of *Acanthobdella* contains no other sensory organs. Their arrangement allows the conclusion that the head region of *Acanthobdella* is very probably formed solely and exclusively by 5 somites. Another indication of this was furnished by the facts determined in relation to the chaetal apparatuses of the head region.

We will now describe the musculature of the two anterior head somites.

In the 2nd somite it consists of the well-developed annular muscle layer (rm) and a few longitudinal muscle bundles (Fig. 38, No. 61). In the mid portion of this somite the annular muscle fibres separate slightly, and the above described sensory organs (sk) project mediad through the gaps. The longitudinal muscle strands which had already been considerably reduced in the 3rd head somite are even more reduced here, especially ventrally. In the anterior portion of the 2nd head somite, we now encounter muscle bundles which constitute a direct continuation of the premedian (pmd), intermediate (int) and paramarginal (pmr) ventral, dorsal and lateral (lb) longitudinal muscle strand. The ventral of these muscle bundles are very poorly developed, and they all disappear completely soon after they enter the 1st somite of the head region; only the paramarginal bundle is more clearly differentiated. The lateral and dorsal bundles are as well-developed as the latter; each of them consists only of two parallel muscle cells. They enter the 1st head somite and soon completely disappear in its pre-oral section. The annular musculature of the 1st head somite contains only a small number of muscle cells which extend mostly in its posterior peripheral section.

This gradual reduction of the musculature in the anterior head somites is easy to understand in view of the general reduction of the somites of the head region of *Acanthobdella.*

In regard to the reduction of the longitudinal musculature, it should be noted that all its longitudinal muscle strands are in the end limited to the above mentioned paramedian, intermediate and paramarginal ventral, dorsal and lateral muscle bundles. The reduction does not go further, and these muscle bundles form the basis for the entire remaining longitudinal musculature of the body of *Acanthobdella.* In the dorsal and lateral muscle bundles it can also be found that their muscle cells form a direct continuation of those muscle fibres which in all trunk somites are closely connected to the ring nerves. However, this is difficult to determine ventrally.

According to F. SCHMIDT (1903), the longitudinal musculature of the anterior body end of *Branchiobdella* has similar characteristics.

The 1st and 2nd head somites of *Acanthobdella* form 2 clearly differentiated innervation areas (Fig. 41, No. 101). The first (1) is supplied exclusively by the nerve (n_1) of the 1st complex of the subesophageal ganglion mass, and for the 2nd, the nerve (n_2) of its ganglion complex plays the same role.

The latter nerve (n_2) initially runs straight cephalad in the inner body mesenchyme above the longitudinal muscles. It then enters the 2nd head somite and divides into 2 branches, one of which ($rn_{2(2)}$) remains in the posterior portion of the only annulus of this somite, while the other ($rn_{2(1)}$) enters its anterior portion. The posterior nerve branch extends over the longitudinal muscle layer to the ventral intermediate line of the body, where it finally enters between the longitudinal and the annular musculature. However, anterior to the ventral paramedian longitudinal muscle strand, the mentioned nerve branch generates a small bundle of fibres which soon reaches the margin between the longitudinal and annular muscles, crosses the paramedian longitudinal muscle strand and again merges with its main branch on the intermediate line. Here on the latter are 1 or 2 ganglion cells and 1 nerve cell of the large tubes. The nerve further extends along the margin between the longitudinal and annular musculature and to the lateral line of the body where at some distance from each other, 2 or 3 pear-shaped ganglion cells are embedded in the nerves. Dorsally the mentioned nerve branch (Fig. 38, No. 61 rn_2; Fig. 41, No. 101, $rn_{2(2)}$) constitutes a typical ring nerve equippped with a nerve cell of the large tubes between the paramarginal (pmr) and intermediate (int) longitudinal muscle strand.

The other branch $rn_{2(1)}$) of the nerve of the 2nd ganglion complex of the subesophageal ganglion mass runs, as mentioned, in the anterior portion of the 2nd head somite, so that the chaetae of this somite are situated between it and the described posterior nerve bundles. Between the longitudinal and the annular musculature it enters anterior to the paramedian longitudinal muscle strand and crosses all 3 ventral longitudinal muscle strands in the typical manner. On the intermediate line of the body a nerve cell of the large tubes lies on it, and near the lateral line are 1 or 2 pear-shaped ganglion cells. Dorsally the described nerve branch forms a typical ring nerve and contains 1 nerve cell of the large tubes which is situated betweeen the paramedian (pmd) and the intermediate (int) longitudinal muscle strand (Fig. 38, No. 61 rn_1).

Thus the 2nd somite of the head region of *Acanthobdella* contains 2 ring nerves whose position corresponds to the anterior and posterior ring nerves of the ordinary neurosomite. The most anterior of them as well as the following 3rd head somite are without the accompanying annular muscle fibre. The nerve fibres of the most posterior nerve branch off to the described sensory organs of the 2nd head somite, so that this nerve also contains the sensitive nerve bundles which in all following somites have differentiated to become a special sensitive nerve. However, this fact and the absence of a separate nerve branch that would be the equivalent of the branch of the posterior ring nerve for the 4th annulus of the ordinary somite present no difficulty for determining the innervation of the 2nd head somite. Its neurosomite contains all the important components of the ordinary mid trunk somite.

Much weaker is the neurosomite of the 1st somite of the head region (Fig. 41, No. 101). Its nerve (the nerve of the 1st ganglion complex of the subesophageal ganglion mass; n_1, $rn_{1(1)}$) initially runs cephalad in the inner body mesenchyme, over the ventral longitudinal muscle; entering its somite it penetrates between the longitudinal and annular musculature where it extends laterad behind the chaetae. On this course the nerve crosses the 3 ventral longitudinal muscle strands, and on the intermediate line of the body it carries a ganglion or nerve cell whose exact nature it is difficult to determine. Reaching the lateral line of the body, it enters the pre-oral, i.e. dorsal portion of its somite, and it can be traced further almost to the median line. The author was unable to determine its connection with the equivalent nerve on the other side, since it is almost impossible to sort out the tangle of glandular, sensory, muscular and mesenchymatous elements. On the lateral line of the body the described nerve sometimes has a ganglion cell.

In the anterior oral portion of the 1st head somite, cephalad of the chaetae, the author sometimes noted an insignificant nerve bundle ($rn_{1(1)}$) which originates ventrally in the vicinity of the median line, probably in the nerve of the 1st ganglion complex of the subesophageal ganglion mass. It runs along the margin between the longitudinal and annular musculature to the lateral line of the body, where a ganglion or perhaps a nerve cell is accumbent to it. This nerve branch soon disappears, and it is generally difficult to determine its relationships accurately.

In both described nerves of the 1st head somite, the typical components of the ordinary neurosomite can hardly be recognized at first sight. But when its characteristics are compared with those found in the neurosomite of the 2nd head somite, there can hardly be any doubt that the 2 nerves of the 1st head somite are equivalent to the two ring nerves of the 2nd somite. Thus the 1st somite of the head region also contains the most important components of an ordinary neurosomite of the mid body, but here they have undergone a maximum degree of reduction. This was to be expected from the outset, taking into account the general reduction of the 1st head somite and in particular the reduction of its musculature.

In describing the nerves of the head region of *Acanthobdella*, the author has thus far completely ignored the lateral nerve. In the 5th, 4th and 3rd head somites it can be easily traced (Fig. 41, No. 101 ln). Only in the vicinity of the lateral pair of chaetae one loses track of it over a varying distance, because it disappears between the other elements of the body wall; but even here it could occasionally be seen clearly. Its relationships are the same as those described for the ordinary mid trunk somites. However, the examination of the lateral nerve becomes much more difficult in the 1st and 2nd somite. As it seems, it continues its course through these two somites as well, but it becomes considerably weaker and finally ends by merging with the anterior nerve bundle of the 1st head somite.

Apart from those described there are no nerves in the body wall of the head region of *Acanthobdella*. This fact again allows us to state – this time with greater certainty – that the head region of *Acanthobdella* consists exclusively of the 5 anterior somites of the body. The cephalic lobe, as it is generally known in the Annelids, has completely disappeared in Acanthobdella.

It now remains to discuss a group of elements which participate in the composition of the body wall of the head region, namely the giant glandular cells of the inner mesenchyme.

As indicated above, the glandular cells situated cephalad of the 3rd somite of the midgut region (14) are sending their secretory ducts (aup) into the anterior body end. As these enter the 5th head somite (5), they divide into 3 clearly defined groups (Fig. 33, No. 3). From these a very thick cluster runs dorsally in the inner body mesenchyme below the longitudinal muscles and mediad of the intermediate longitudinal muscle strand (int); a second insignificant cluster is situated in the inner body mesenchyme below the longitudinal muscles dorsad of the lateral line, and a third cluster of medium thickness lies ventrally in the inner body mesenchyme above the paramedian longitudinal muscle strand (pmd_1).

In the 5th head somite only some of the secretory ducts separate from the lateral cluster, and here these ducts open outwardly at the lateral pair of chaetal sacs. In the 4th head somite, too, this group generates only a few secretory ducts which extend to the lateral pair of chaetae, around which their outer openings are situated. The other secretory ducts of the lateral cluster enter the 3rd head somite where they terminate in a very similar fashion.

A small number of secretory ducts come from the dorsal and ventral clusters in the 5th head somite (Fig. 33, No. 3). The bundle of secretory ducts, formed dorsally, then enters the dorsal coelom section, naturally surrounded by a peritoneal sheath, and extends cephalad until it enters the esophageal wall in the 4th or posterior section of the 3rd somite. Its further course lies in the corresponding upper quadrant of the section of the esophagus (Fig. 38, No. 66). In the same manner as the described bundle, the bundle of secretory ducts that comes from the ventral cluster also enters the ventral coelom section at the margin between the 5th and 4th head somites; it penetrates the esophageal wall near the margin between the 4th and 3rd head somite, where it continues in the corresponding lower quadrant. This bundle of secretory ducts of the giant glands will be discussed again below in connection with the intestine.

All other secretory ducts (aup) of the ventral cluster extend through the 4th head somite into the 3rd (Fig. 33, No. 2) where they represent an insignificant bundle that runs to the ventral median line of the body and opens toward the outside in the middle portion of the 3rd head somite. Another such bundle separates from the ventral cluster in the 2nd head somite and opens toward the outside in the middle portion of the latter on the ventral median line. The other secretory ducts of the ventral cluster enter the 1st head somite, where they end directly behind the oral opening, i.e. on the ventral median line of the body.

In the 4th and 5th head somite (Fig. 33, No. 2) the secretory ducts of the dorsal cluster, after sending the bundle to the esophagus, separate into 2 smaller clusters, one of which (situated on the median side) again divides in two. The outer bundle curves ventrad in the 2nd head somite, and most of its secretory ducts lead outside in the middle portion of this somite between its ventral and lateral pair of chaetal sacs; the smaller number of ducts terminate in the same fashion dorsally of the lateral pair of chaetae. The two clusters formed from the inner bundle of secretory ducts enter the 1st head somite; the larger extends ventrad, and its secretory ducts lead to the outside in this head somite between the ventral and lateral pair of chaetal sacs, i.e. laterad of the oral opening. The smaller cluster does not run toward the ventral body surface, since its secretory ducts have their outer openings in the dorsal pre-oral portion of the 1st head somite between the two lateral pairs of chaetal sacs.

This indicates that the entire surface of the 1st somite is far more generously endowed with the secretory ducts of the giant glandular cells than the other somites. In the 2nd head somite these secretory ducts terminate over the entire ventral and lateral body surface; in the 3rd the openings can be seen laterally and ventrally only on the median line of the body; in the 4th and 5th head somite they are limited to the lateral line alone. All this seems to indicate that the giant glandular cells of the inner mesenchyme must be closely related to the function of the anterior body end of *Acanthobdella* as a sucker, just as the glands always present in the suckers of the other Hirudinea are of similar importance. It should be mentioned here that *Haplotaxis* is endowed with well-developed glandular cells in the vicinity of the oral opening.

The bundles of the discussed secretory ducts of *Acanthobdella* also show a certain differentiation in relation to the area where they lead to the outside. Thus the dorsal cluster consists of secretory ducts closely related to the 1st and 2nd head somites; the ventral cluster contains bundles which open toward the outside on the ventral median line of these and the 3rd head somite, and the lateral cluster finally combines the secretory ducts of the 3rd, 4th and 5th head somites belonging to the lateral line of the body.

The dorsoventral muscles of the head end of *Acanthobdella* seem to be specially adapted to its sucker function. They are described below in connection with the diagonal muscles and with the coelom and dissepiments of the head somites (Fig. 35, No. 18).

Only ventrally does the dissepiment (dsp_5) between the 5th head somite and the 1st preclitellar somite (6) constitute a muscle arc (Fig. 41, No. 106) similarly to the other preclitellar somites, i.e. on each side of the ventral median line of the body extends 1 muscle cell (Table 35, No. 18 dsz_5) which then passes the coelom in a mesenchyme strand (oe) and ends in a corresponding lower quadrant of the same. It should be noted that the described section of the dissepiment has shifted slightly caudad and is thus not situated on the somite margin but already in the first annulus of the 1st preclitellar somite. The dorsal dissepiment sector is formed by 2 muscle cells (pr_4), i.e. one on each side, which attach themselves with one end to the corresponding quadrant of the espohagus on the margin of the respective somites. Their further course is determined by adaptation to their special function: they constitute the posterior pair of protractors for the esophagus. Distinguishable from the esophageal wall, each of these muscle cells enters the coelom where it extends to the 3rd head somite, from whose posterior margin it enters the inner body mesenchyme until it finally attaches itself to the integument on the dorsal paramedian line (Fig. 35, No. 18). The antagonists of this pair of protractors are the ventral muscle cells of the dissepiment which thus can be called the retractors of the esophagus.

In the 5th head somite the coelom (c) very considerably broadens laterad, anterior of the described dissepiment, and it extends directly to the longitudinal muscle strands which are situated there (Fig. 33, No. 3; Fig. 41, No. 106 c_5). The coelom uninterruptedly continues as a thus enlarged cavity into the 4th and 3rd head somites, where it is traversed only by the dissepimental (dsz, pr) and dorsoventral (dvm) muscles (Fig. 35, No. 18). In the 2nd head somite, however, the coelomic cavity is reduced, since here the chaetal sacs (bsz_1, bsz_2) of the two anterior head somites protrude greatly, and since the inner body mesenchyme increases in size because (due to the general reduction of somite size) it contains a large number of glandular secretory ducts as well as the well-developed sensory organs (Fig. 33, No. 2). Because of this accumulation of glandular ducts and sensory elements in the inner mesenchyme, the coelom (c) of the 1st head somite disappears almost completely and only remains around the intestine (Fig. 38, No. 63) and the proximal portions of the chaetal sacs. All described formations that project into or traverse the coelom are, of course, covered by a continuous coelothelial layer.

In the posterior portion of the 5th head somite the coelom is usually traversed by an ordinary dorsoventral muscle cell (Fig. 35, No. 18 dvm_5) whose ends attach themselves to the integument of the 4th somite annulus on the intermedian line of the body. Here, this cell is quite independent of the dissepiment, while in the following (i.e. preclitellar) somites it always participates in the composition of the dissepiment. The coelom of the 5th head somite is also traversed by a very well-developed dorsoventral muscle cell (dvm_5) whose processes attach themselves to the integument of the 1st and 2nd somite annulus on the paramedian line. We will see below that such thick dorsoventral muscle cells are generally characteristic for the head region of *Acanthobdella*.

The nucleate portion which appears oval in section (Fig. 38, No. 62 mz, 63 dvm) is covered over its entire periphery by the fibrillar-contractile layer which at both ends of the cell splits into a large number of insignificant muscle fibres (Fig. 38, No. 67 dvm).

As usual, the diagonal muscle cells (sm) occur as 1 pair in each annulus of the 5th head somite (Fig. 35, No.18). In the 1st and 4th annuli they are quite typically developed, while in the 2nd and 3rd somite annuli they are – as already described – closely related to the chaetal sacs of the respective somite, for which reason the ventral point of attachment of the most posterior pair has been shifted into the 2nd annulus, to the distal portion of the ventral pair of chaetal sacs.

In the anterior portion of the 1st annulus of the 5th head somite is the ventral muscle arc of the dissepiment which belongs to the margin between the above mentioned and the 4th head somite. Its development is the same as that of the following dissepiment. Here the dorsal dissepiment muscles also form a pair of protractors of the esophagus, namely the middle pair (pr_3); again there is a muscle cell on each side that can be distinguished from the esophageal wall on the margin of the 5th and 4th head somites near the lateral line of the esophagus, extends cephalad and laterad in the coelom (Fig. 33, No. 2; Fig. 35, No.18), and attaches itself to the integument at the margin of the 3rd and 2nd head somites on the dorsal paramarginal line.

In the 4th head somite on the paramedian line of the body is only one dorsoventral muscle cell (dvm_4). It is extremely well-developed: it begins in the anterior portion of the 1st somite annulus, occupies the entire 2nd annulus and ends in the 3rd annulus. Another such muscle cell, also very well-developed (dvm_4), belongs to the intermediate line of the body (Fig. 35, No.18). Judging by the attachment point of the muscle fibres sent out by it, the majority of which insert in the vicinity of the paramedian line, it can probably be regarded as an ordinary dorsoventral muscle cell which because of the shortening of the somite and the strong development of the adjacent cell has been shifted into the same lateral plane as the latter.

The 4th head somite contains 2 diagonal muscle cells (sm) on each side, and these are – as mentioned – closely related to the chaetal sacs of this somite; the posterior cell has shifted slightly cephalad.

The muscle arc situated in the 1st annulus of the 4th head somite of the respective dissepiment has the same characteristics that were described above for the following head somites. Its dorsal section on the other hand is represented by the 2 most anterior protractor pairs ($pr_{1,2}$) of the esophagus, whose cells can be distinguished from the wall of this intestinal section on the margin between the 3rd and 4th head somites (Fig. 35, No.18; Fig. 38, No. 63, 67). Beginning in the corresponding upper quadrant of its section, the two protractors traverse the dorsal coelom portion, extend laterally past the supraesophageal ganglion mass and end at the integument of the anterior portion of the 2nd head somite near the dorsal paramedian line of the body (Fig. 33, No. 2).

We see therefore that all described dissepiments of the head region are quite similar, in fact almost identical, and that there can be no doubt about their nature. Further cephalad, namely between the 3rd and 2nd and between the 2nd and 1st head somites, the dorsal portions of the dissepiments remain undeveloped. Ventrally they are either also completely absent or represented by only those few muscle cells ($dsz_{1,2}$) which come from the median line of the body and enter the esophageal wall in the pharyngeal nerve ring, i.e. in the anterior portion of the 3rd head somite (Fig. 35, No. 18). Such characteristics would be quite understandable in view of the fact that the supraesophageal and subesophageal ganglion mass of *Acanthobdella* is situated in the 3rd head somite. The former could assume their original position, generally typical for Annelids, anterior to the 1st body dissepiment, only together with a caudad displacement of the two anterior dissepiments into the 3rd head somite, or after atrophy of these dissepiments into the latter somite. Similarly the displacement of the 1st and 2nd ganglion complexes of the subesophageal ganglion mass, which, as mentioned, actually belong to the 1st and 2nd head somite, could have happened through either the displacement or the reduction of the ventral portions of the two most anterior dissepiments. The latter process, i.e. the atrophy of the dissepiments, does indeed seem to have happend in the two anterior head somites of *Acanthobdella*.

The above mentioned total atrophy of the dissepiments, or the fact that only relatively unimportant muscle strands remain of them, is apparently closely related in the head region – as in the preclitellar somites, although to a lesser degree – to the function of the anterior body end as a sucker. During strong contractions, particularly of the dorsoventral muscles, as they occur during suction, a considerable quantity of coelomic liquid in the anterior trunk somites must be able to change its position quickly, and this can only be achieved by the atrophy of the massive dissepiments. On the other hand, the development of a movable esophagus, as it is useful for food intake by suction, may also have contributed much to this modification of the dissepiments.

In the 3rd head somite the dorsoventral musculature (dvm_3), similarly to that in the 4th, is represented by one cell on the paramedian line of the body and another on the intermediate line (Fig. 35, No. 18). The two cells are very well-developed , and the first (dvm) lies directly behind the pharyngeal nerve ring (Fig. 38, No. 67). The anterior of the 2 diagonal muscle cells (sm) is closely related to the lateral pair of chaetal sacs – as described for the more posterior somites. The posterior cell, on the other hand, is not closely related to the ventral pair. The typical relationship to the latter is shown by the diagonal muscle cell which attaches itself to the integument near the anterior margin of the 4th somite. However, it is very difficult to decide whether this cell belongs to the 3rd head somite or whether it represents the most anterior diagonal muscle cell of the 4th head somite (Fig. 35, No. 18).

The dorsal attachment points of the dorsoventral and diagonal muscle cells of the 1st and 2nd head somite have all more or less shifted caudad as the result of the above described structural situation in the anterior body end. Nonetheless the muscle cells typical for the head somites can be located here without difficulty (Table 35, No. 18). Thus on the paramedian line of the body in the 2nd somite is a well-developed dorsoventral muscle cell (dvm_2) that is situated directly anterior of the pharyngeal nerve ring (Fig. 33, No. 2; Fig. 38, No. 63). Its ventral processes attach themselves to the integument of the 2nd somite, while the dorsal processes enter into the anterior section of the 3rd somite. The dorsoventral muscle cell (dvm_2) on the intermediate line is represented in the 2nd head somite by a poorly-developed cell which one may perhaps already count to the diagonal musculature of the mentioned somite (Fig. 35, No. 18). The latter (sm) is here formed by 3 typical cells, the most posterior of which may perhaps belong to the 3rd somite and extends to the ventral pair of chaetal sacs. The middle cell, as in the 3rd head somite, is almost completely independent of the chaetae, while the anterior cell runs toward the lateral pair of chaetae. Dorsally all these cells attach themselves laterally or dorsally to the integument of the 3rd somite. In the anterior section of this somite the diagonal muscle cells of the 1st somite also attach themselves, the most anterior of which is closely related to the lateral pair of chaetal sacs, the most posterior to the ventral pair. The latter muscle cell may already belong to the 2nd somite. As in the other somites, 2 dorsoventral muscle cells (dvm_1) are present in the 1st somite (Fig. 35, No. 18). Both insert ventrally on the median line of the body, immediately behind the oral opening. Dorsally one of them, relatively very unimportant, attaches itself to the integument of the 2nd head somite on the paramedian line, while the other, well-developed, extends to the intermediate line of the same somite.

In addition to the described muscles, the head region of *Acanthobdella* contains a bundle (mf*) that is formed by 2 small muscle cells. In the anterior median part of the supraesophageal ganglion mass, it extends through the dorsal coelom (c) to the integument of the 2nd head somite, to which it attaches itself on the median line of the body (Fig. 38, No. 59). Finally there are 2 bundles of unimportant muscle cells, 1 on each side, which extend from the margin of the oral opening dorsad to the median line of the anterior portion of the 3rd head somite. These two muscle bundles differ slightly from all other above described muscles of the head region in that their cells have a very compact appearance in spite of their insignificant size.

Summarizing the above facts, we can conclude that the dorsoventral and diagonal muscles in all head somites resemble each other and are of typical development. The former are extremely well-developed and of extraordinary thickness, so that the entire head region is as much filled with the muscle fibres coming from these cells as is the case in the other Hirudinea, where this is caused, however, by a very considerable number of individual dorsoventral muscle cells. This development in *Acanthobdella* is, of course, a necessary result of the anterior body end's function as a sucker. The diagonal muscle cells, which are closely related to the chaetal sacs of the head somites, are equally adapted to the special circumstances of the head region of *Acanthobdella*.

Finally, the behaviour of the dissepiments, the dorsoventral and diagonal muscles of the head region, indicates that in *Acanthobdella* this region is formed solely and exclusively by the 5 most anterior trunk somites. No formations are present here which are not associated with the latter, and in the author's opinion, the muscle bundle of the supraesophageal ganglion mass and the two bundles coming from the oral opening can be of no importance in this relationship.

As the end result of all previous conclusions obtained after a detailed discussion of factual material, it can be established that the head region of *Acanthobdella* consists exclusively of the 5 most anterior head somites and that the cephalic lobe found in the other Annelida has disappeared. The 5 head somites are innervated in a strictly metameric fashion by the 5 most anterior ganglia of the ventral cord, which are here represented by the 4 ganglion complexes of the subesophageal ganglion mass and the 1st ordinary ventral ganglion. The supraesophageal ganglion mass therefore proves to be a formation *sui generis* which is homologous neither to the subesophageal ganglion mass nor to an ordinary ganglion of the ventral cord; rather it has the function of a non-metameric formation to which in this case no special body part corresponds.

The supraesophageal ganglion mass of *Acanthobdella* is definitely the equivalent of the brain in the Oligochaeta and the other Annelida where the brain is also a non-metameric organ without any close relationship to the cephalic lobe. While the cephalic lobe has obviously completely regressed in *Acanthobdella*, the corresponding central sector of the nervous system has been retained in the body as its nerve centre. However, the formation of ganglion cell clusters in the supraesophageal ganglion mass must be regarded as the result of a general differentiation process to which all nerve centres of *Acanthobdella* were subjected, regardless of whether they were originally metameric or non-metameric structures.

The supraesophageal and subesophageal ganglion mass in the other Hirudinea is, as indicated above, quite homologous to that in *Acanthobdella*, but has been shifted even further caudad – probably because of the final development of the anterior sucker. As the author has maintained earlier (LIVANOW, 1904, 2), in this case, too, the development of ganglion cell clusters in the supraesophageal ganglion mass is connected with the clustering of ganglion cells in the nerve centres, generally very widespread in Hirudinea, and it should under no circumstances be interpreted to mean that the supraesophageal ganglion mass had been formed by the fusion of metameric sections. It definitely represents the non-metameric part of the central nervous system of the Hirudinea which corresponds to the non-metameric most anterior body section that has disappeared in *Acanthobdella*. Thus the anterior body annuli of Hirudinea, which are innervated by the supraesophageal ganglion mass, are homologous to the cephalic lobe in Oligochaeta, which is completely confirmed by the findings of the author (LIVANOW, 1904, 2) after his examination of the anterior body end of Hirudinea.

The annulation of the cephalic lobe in Hirudinea is not important in this respect, since we find the same already in *Haplotaxis*, where this phenomenon is apparently connected with the general formation of skin annuli over the entire body. Similarly, the distribution of sensory organs in the cephalic lobe of Hirudinea according to ordinary body lines may have to be regarded as a characteristic that was probably an adaptation of the arrangement of neuromuscular structures along the same longitudinal lines in the pre-oral and post-oral body sections, as it must have been originally the case in all Annelida.

Another peculiarity should be mentioned here in which the 1st trunk somite of *Acanthobdella* differs from that of the Oligochaeta, namely the fact that this somite has a well-developed chaetal apparatus, while the absence of chaetae in the 1st somite is a characteristic of the Oligochaeta. In view of the undeniable general homologies which exist between *Acanthobdella* and the Oligochaeta on the one hand and *Acanthobdella* and the other Hirudinea on the other hand, there can hardly be any doubt that the somite is really the same one in both cases.

Finally the author wishes to make some comments in regard of the ideas expressed by C. WHITMAN (1892) on the nerveous system and the head region of the Hirudinea. WHITMAN wrote: "The head (of *Glossosiphonia hollensis* Whitm.) consists either 1) of a non-metameric lobe plus a number of metameres originally belonging to the trunk, or 2) of such metameres only, the non-metameric head-element of the ancestral form having been lost or incorporated in the first metamere". On the basis of his examinations, WHITMAN further claimed that the non-metameric body section of the Hirudinea had undergone a full regeneration: "The morphological equivalence of segment I with the following segments is evident to a degree that is really astonishing. It makes no departure from the typical trunk-segment which is not led up to through gradations represented in the segments immediately following it ... We find nothing whatever in segment I, which is not repeated in other segments, and hence conclude that the thirty-four segments of *Clepsine* are strictly homodynamous". All these conclusions of WHITMAN, although many authors have accepted and apparently confirmed them, are based on insufficient morphological evidence, as the author has already shown (LIVANOW, 1904, 2), and now we can categorically state that they are wrong. The non-metameric cephalic lobe is present in all Hirudinea with the only acception of *Acanthobdella* And the same applies to the following thesis of WHITMAN: "The ganglionic centres of the ventral cord are simple repetitions, element for element, of the 'brain'. The nervous system is made up of segments of equal morphological value throughout. It must be regarded then either as a series of 'brains', or as a series of ventral neuromeres, one or more of which have been carried secondarily to the dorsal side, and which here take the place of a brain that has been lost or confounded with the metameric system. That a portion of neuromere II has suffered transposition from the ventral to the dorsal side is certain". The author must dispute all these conclusions of WHITMAN on the basis of newly acquired evidence. The supraesophageal ganglion mass of the Hirudinea is a non-metameric structure that has absolutely nothing to do with the ganglia of the ventral cord, since the latter do not participate in any way in the formation of the supraesophageal mass.

9. The attachment disk region

Earlier authors who wrote about the attachment disk region, have referred only to the external morphology of this body section, and they have already been cited above. The internal structure has been completely disregarded in earlier studies.

Even in the posterior annulus of the 5th somite (24) of the hindgut region, some changes can be noted in the longitudinal musculature; some muscle bundles separate from the others and shift more mediad in the inner body mesenchyme (Fig. 34, No. 13). This change takes place in the ventral and dorsal longitudinal muscle strands on the median line as well as in those that extend ventrally mediad from the paramedian (pmd_1), intermediate (int_1) and paramarginal (pmr_1) longitudinal muscle strands, but dorsally laterad from the same strands (pmd, int, pmr), and ventrad from the lateral strand (lb).

The 6th somite (25) of the hindgut region that borders on the attachment disk region already has very pronounced reduction characteristics. Here, apart from the reduction of the above described external annulation, the annular muscle fibre of the anterior ring nerve and the nerve branch of the 4th somite annulus have disappeared. The associated ganglion of the ventral cord seems to be almost completely fused with the anal ganglion mass. In accordance with the reduction of the coelom cavity (c) the inner body mesenchyme (ms) of the respective somite is strengthened, and thus the longitudinal muscle fibres expand mediad by acquiring new muscle fibres in addition to those situated peripherally (Fig. 34, No. 14; Fig. 35, No. 16).

In the posterior section of this somite and at the beginning of the attachment disk region, it can be seen that the coelom has completely atrophied (Fig. 41, No. 108) and that the longitudinal musculature (lm) expands in fan-like fashion from the centre of the attachment disk toward the periphery (Fig. 35, No. 16); these muscle strands are separated from each other by fairly large spaces filled with mesenchyme (Fig. 35, No. 15). This is accomplished as follows: 2 ventral muscle strands, 1 on each side of the median line, merge on the median line and form a muscle bundle that has a fan-shaped appearance in section. Such bundles are also formed by the muscle strands lying on the paramedian line ventrad and mediad of the former bundle, and these bundles take their position laterad of the median bundle. Between the paramedian strand and the lateral line of the body is the longitudinal muscle bundle that is formed by the intermediate ventral strand and the strand lying laterad of the same. However, the ventral paramarginal longitudinal muscle strand usually separates from the latter and merges with the lateral longitudinal muscle strand. These and the dorsal paramarginal longitudinal muscle strand form a fan-shaped longitudinal muscle bundle lying dorsally on the lateral line of the body. Between it and the dorsal median longitudinal muscle bundle is another fan-shaped longitudinal muscle bundle formed of the intermediate and paramedian longitudinal muscle strand.

There are frequent deviations from the type of longitudinal muscle distribution found in the attachment disk region. For example, a dorsal median longitudinal muscle bundle, usually poorly developed, can occur, or the dorsal longitudinal muscle strands may group themselves differently to form the fan-shaped bundles.

The described strong development of the longitudinal muscle strands occurs when beginning with the 6th somite of the hindgut region, the ordinary muscle fibres of the longitudinal strands are joined by new muscle cells which enter between the longitudinal muscle fibres with their anterior, usually ramified end, fasten themselves to the integument and continue to their course in the longitudinal muscle strands (Fig. 35, No. 16). Except for a few peripherally situated fibres, almost all longitudinal muscles insert their ends at the integument of the attachment disk concavity on whose surface they are very regularly distributed. In this manner, most of the longitudinal muscle fibres assume a more or less pronounced diagonal course, depending on their attachment point in the attachment disk concavity. The few peripheral fibres (lm*) on the other hand retain their earlier course and thus reach the posterior seam of the attachment disk; here they penetrate between the annular muscles on which they run distad from the annular musculature (rm) and radially toward the centre of the attachment disk, while their ends extend to the concavity of the attachment disk. Therefore, no nuclei can be seen in the longitudinal muscles of the attachment disk concavity.

The annular muscle layer (rm) in the entire attachment disk region is developed evenly and as in other body sections, except that at the attachment disk concavity it lies mediad of the peripheral longitudinal muscles (lm*). A peculiarity is an annular muscle bundle (rm*) that lies slightly mediad of the seam of the attachment disk, on its concavity. It is separated from the other annular muscles (although directly adjacent to them) because it lies mediad of them in the mesenchyme of the disk. It consists of 6 muscle cells, 3 on each side of the median line. Nothing can be said about the significance and origin of this muscle ring that is conspicuous by its position.

The diagonal musculature is completely absent in the attachment disk region.

In addition to the described muscles, the latter contains special muscle fibres (mz) that extend from the outer wall of the attachment disk to the inner, i.e. concave wall (Fig. 35, No. 16). They are small muscle cells with slightly ramified ends built according to Hirudinea type except that their nucleate section in one half of the periphery has no contractile-fibrillar layer. These muscle cells probably constitute none other than longitudinal muscle fibres whose attachment points are greatly displaced. As described, the longitudinal musculature contains fibres which on one side insert near the attachment disk centre and on the other side attach themselves to the integument of the 6th somite of the hindgut region, i.e. they take a more or less diagonal course. Forming an uninterrupted row together with these are muscle cells which already attach themselves distally at the integument of the attachment disk region, and this phenomenon reaches its culmination point in muscle fibres (mz) that are fixed almost at the seam of the attachment disk itself, while their other end attaches itself to the concavity of the latter. The middle sections of these cells deviate from the annular muscles and already lie freely in the mesenchyme of the disk.

By and large the attachment disk region contains the muscles that usually occur in the ordinary trunk somite; however, these muscles have more or less adapted to the function of the attachment disk and no longer show traces of metamerism.

The skin epithelium of the attachment disk region also shows no signs of metamerism. On the outside of the disk the skin epithelium retains its usual appearance; it contains a few scattered sensory buds which, however, are absent on the concavity. A specific characteristic of the sensory buds is that the epithelium is perforated by an extraordinary number of glandular secretory ducts. Since these project between the annular and longitudinal musculature, they are arranged in groups, and inside these grids, the epithelium forms inward proliferations between the muscles. These inward proliferations of the epithelium are formed mostly by very young glandular cells which are therefore still embedded in the epithelial layer. The cells to which these secretory ducts belong have already been described above. It should only be noted here that while all glandular cells situated in the anterior half of the body lead to the outside in the head region, those behind the 3rd mid trunk somite (14) terminate on the attachment disk concavity.

The inner mesenchyme of the attachment disk region is tightly filled with such glands, and only at the outer attachment disk wall are there a few scattered pigment-fat cells.

The central nervous system of the attachment disk region forms the last ganglion mass (agn) of the ventral cord (Fig. 33, No. 1; Fig. 41, No. 105). It is embedded in the blind coelom sac that lies behind the anal opening. Cephalad this ganglion mass borders directly on the ventral ganglion of the 6th somite (25) of the hindgut region, and occasionally the latter completely merges with it. In rare cases the ventral ganglion of the 5th somite (24) of the hindgut region is also fused with this ganglion mass. However, this merger only represents an external manifestation of the approximation of these ganglia to each other, since their morphological independence and that of the associated connectives is completely maintained.

The anal ganglion mass in the narrower sense forms an elongated body divided into 4 well-defined sections (Fig. 41, No. 105).

In the most anterior section are ventrally 2 successive median clusters (mp_1) of ganglion cells , and laterally on each side 2 lateral clusters (lp_1). The latter lie at an angle to each other, i.e. the anterior lies somewhat higher than the posterior. All clusters represent oval masses. The connective trunks (cn) have fused with each other along the entire distance, and at the posterior margin of the anterior median cluster they each contain one glia cell on each side of the median line. Ventrad, 2 nerves (n_1) extend from the central fibre mass of the said section. Therefore this section of the anal ganglion mass has almost no structures that deviate from the ordinary ganglion of the ventral cord, which is also a clear indication of its morphological significance. It is a formation that is quite homologous to the ordinary ventral ganglion. The fact that only 2 instead of 3 nerves extend from it on each side, shows that the nerves have fused, as is often the case due to local structural conditions. These nerves extend to the median ventral muscles without showing any indication of ring nerves or any other differentiation, and this can be explained by the complete fusion and the resulting disappearance of individuality of the different somites in the attachment disk region.

In the mesenchyme layer of the anal ganglion mass 2 muscle cells run dorsally, one on each side of the median line, whose nucleate parts lie directly anterior to this section of the anal ganglion mass. This characteristic also resembles the situation in the ordinary ventral ganglion.

Finally the ganglion cell clusters of the described section of the anal ganglion mass are directly followed by those of the next section. Nevertheless it can be seen that on the margin between them the connective trunks separate from each other over a very short distance, and here they each contain 1 glia cell whose position corresponds to that of the ordinary connective cells, but they are embedded somewhat laterally in the connective trunks.

After this separation the connective trunks unite again in the area of the 2nd section of the anal ganglion mass. Ventrally in this section are 2 median clusters (mp_2) of canglion cells lying behind each other; laterally, too, 2 lateral clusters (lp_2) are present, one on each side of the median line, and dorsally above these, embedded in the mesenchyme, are 2 muscle cells whose nuclei are situated just before the said section.

It can therefore be stated that the just described 1st section of the anal ganglion mass is fully identical, i.e. that the 2nd section of the anal ganglion mass is also homologous to an ordinary ventral ganglion. However, one very clear difference is that from this 2nd section only one single nerve (n_2) extends which originates in the most anterior part of the corresponding section of the central fibre mass. Its course very significantly deviates from the characteristics of the ordinary nerves of the ventral cord in that it runs to the muscles that lie on the ventral intermediate line. Similar characteristics are found in the nerves of the 1st section of the just described anal ganglion mass.

Behind the 2nd section the separation of the connective trunks is not very pronounced; laterally each of them contains one glia cell, i.e. a connective cell.

The 3rd section of the anal ganglion mass is quite similar to the described 2nd section in regard to the central fibre mass and its 2 glia cells and in regard to the position of the 4 lateral ganglion cell clusters (lp_3), the 2 dorsal muscle cells and the ending of the nerves (n_3). The only difference lies in the median clusters (mp_3) which are situated not behind each other, but at a certain angle to each other, i.e. one somewhat to the right, the other left of the median line. This is certainly caused by the fact that the ganglia in the anal ganglion mass are greatly crowded, a characteristic resembling the situation in the subesophageal and supraesophageal ganglion mass in the other Hirudinea.

Thus the 3rd section of the anal ganglion mass of *Acanthobdella* also seems to be homologous to an ordinary ganglion of the ventral cord. As those of the 2 anterior sections, the 2 nerves (n_3) of this section show no signs of any metameric relationship and run directly to the muscles on the lateral line of the body (Fig. 35, No. 16).

An interesting peculiarity in the 3rd section of the anal ganglion mass is the fact that the posterior median cluster of ganglion cells is often virtually united with one of the posterior lateral clusters or, to state it more correctly, that these clusters look poorly differentiated from each other. This may have happened as the result of the reduction of individual ganglion sections, along with the reduction of somites in the attachment disk region (Fig. 41, No. 105).

To a greater degree the same phenomenon occurs in the 4th section of the anal ganglion mass. The following are present: 2 median clusters (mp_4), one on each side of the median line, and 4 lateral clusters, the posterior of which on each side occupies the corresponding part of the posterior surface of the central fibre mass and is accumbent to the median cluster, while the anterior cluster (lp_4) lies on the dorsal and lateral surface between the posterior lateral cluster of the 3rd section and that of the 4th. Usually the demarkation between the median cluster and the corresponding lateral cluster is very poorly defined or almost absent (Fig. 41, No. 105).

The dorsal muscle cells are completely absent in the 4th section. The central fibre mass behaves in this section as in the previous section: it contains ventrally 2 glia cells arranged symmetrically to the median line. Between the 4th and 3rd section the connective trunks separate over a very short distance, and laterally in each trunk is one connective cell.

Similarly as from the 3rd and 2nd sections, 2 nerves (n_4) extend from the 4th section of the anal ganglion mass, running to the muscles situated on the dorsal intermediate line. Caudad 2 nerves (n^*) extend from the central fibre mass which look like a direct continuation of the 2 connective trunks. At each of their exit points 1 glia cell is accumbent to the fibre mass, rsembling the described cells. The nerves themselves run to the muscles which are situated on both sides of the dorsal median line. It is quite natural that the 2 anterior nerves of the 4th section of the anal ganglion mass resemble those of the previous sections, since they are homologous formations. In the posterior nerves, however, although their behaviour is similar, a homology with the former is doubtful, and the question about their morphological significance has to remain unsanswered for the time being. In any case, there is no doubt that even in the 4th section of the anal ganglion mass, there is a homology with the ordinary ganglion of the ventral cord.

Thus the anal ganglion mass of *Acanthobdella* originates in the fusion of 4 ganglia which are homologous to the ordinary ganglia of the ventral cord. In addition, these may be joined anteriorly by 1 or 2 ganglia of the hindgut region.

While neither the composition of the body wall and its innervation nor the characteristics of the coelom provide any information as to the morphological significance and the metamerism of the attachment disk region of *Acanthobdella*, the central nervous system does furnish unequivocal proof that this region originated in the fusion of 4 metameric sections, i.e. 4 trunk somites. If we also take into account that the attachment disk in the other Hirudinea, as ontogenetic evidence proves without a doubt, was formed out of 7 trunk somites and yet no traces of the relevant metamerism remain in the adult stage except in the central nervous system, we can establish that the formation of the attachment disk region in *Acanthobdella* is completely homologous to the situation in the other Hirudinea.

As will be seen below, the blood vessel system of *Acanthobdella* also furnishes important evidence confirming the above findings.

While there is undoubtedly an analogy in how the attachment disk of *Acanthobdella* and the other Hirudinea was formed, there remains nevertheless an important difference when the structure of this body section is compared. The attachment disk of the Hirudinea is formed by 7 trunk somites and constitutes a well-differentiated, clearly separated organ which is positioned parallel to the trunk axis. In *Acanthobdella*, on the other hand, only 4 trunk somites participate in the formation of the attachment disk, and the latter is not cleary differentiated at all. This as well as its vertical position in reference to the longitudinal axis of the body indicates that the attachment disk of *Acanthobdella* is actually more closely related to that of *Branchiobdella*. In comparison with both of these, the organ in question is at a higher stage of development in the other Hirudinea.

10. The intestinal tract

The first information about the intestinal tract of *Acanthobdella* was supplied by E. GRUBE (1851) who wrote: "The digestive tract rests directly against the muscular wall of the body ... it extends straight from fore to aft, everywhere corresponding in thickness to the body except in the anterior part which forms the esophagus that is very narrow and slightly coiled, especially in the beginning. It as well as the other part of the digestive tract is attached in stages by ligaments to the body wall ... causing a series of successive cavities or chambers connected with each other through wide openings; I counted about 8 of these. There are no special typhlosoles, and externally no delineation could be observed between stomach and gut ... Its content was a uniform magma resembling coagulated blood". A more detailed description was given by A. KOWALEWSKI (1896, pp. 268 and 269), who wrote:

> „Le canal intestinal commance par l'ouverture buccale placée sous un prolongement conique de la tête qui à la forme d'une lèvre supérieure, et qui conduit dans la cavité buccale. Dans cette cavité s'ouvrent des deux côtés deux paires de glandes salivaires, et postérieurement commence l'oesophage ou la trompe qui se prolonge jusqu'au troisième segment du corps. Cette trompe est un organe extrêmement musculaire et possède plusieurs muscles spéciaux pour la tirer en avant. . . . Du 3. segment jusqu'au 16-me se prolonge l'intestin médian en formant des petits proéminences ou renflements dans chaque segment. Du 16-me segment jusqu'à l'anus se trouve l'intestin terminal. . . . Tout le canal intestinal médian est rempli par le sang des poissons avec leurs corpuscules sanguins contenant les noyaux. Dans l'intestin terminal les noyaux se disparaissent et on trouve souvent des petits cristaux se colorant en rouge vif par l'éosine."

As described above by the present author, the intestinal tract of *Acanthobdella* begins in the middle of the 1st head somite, with an oval buccal opening (m) about 60-50 μ in length and 20-40 μ in width (Fig. 33, No. 1; Fig. 35, No. 17,18). This rather wide opening leads into the buccal cavity (mh) which is formed by a simple invagination of the skin epithelium (Fig. 38, No. 63). Over a short distance this invagination of the epithelium is followed by the circular muscle layer (rm*) of the skin which thus forms the circular musculature of the buccal cavity. Here are only a few circular muscle fibres lying vertically above each other. In the upper part of the buccal cavity these muscles are absent, but resting against its epithelium are radial muscle fibres which will be further discussed below. The length of the buccal cavity is about 80 μ. Its epithelium has no peculiarities in comparison with the ordinary skin epithelium, other than the fact that it contains neither glandular cells nor secretory ducts.

Projecting into the buccal cavity is the pharynx which in its beginning section represents the epithelial annular fold (Fig. 38, No. 63 phf). Depending on the degree of invagination or outpouching of the foregut, this fold encompasses either the whole buccal cavity (Fig. 38, No. 63) or only a greater or lesser part of the same. The epithelium of the fold, which constitutes a direct continuation of the buccal cavity epithelium, differs from the latter by the elongated shape of the cells between which no glands or secretory ducts are present. In the basal section of the fold, the body mesenchyme (ms*) inserts over a short distance. Thus muscles (lm*) enter the fold which at the distal pharynx sector extend longitudinally in pairs in each quadrant of the section. In order to leave the fold, these muscle cells form a sort of arc around the upper sector of the buccal cavity. The nucleate sectors of the 4 muscle cells of the posterior, i.e. lower quadrant lie in the pharynx itself, and only their ends enter the body mesenchyme where they extend radially caudad. The 4 muscle cells which extend radially cephalad have their nuclei already in the body mesenchyme, and they attach themselves to the dorsal intermediate line of the 1st head somite near its posterior margin. All these muscles are probably nothing but the remnants of the radial pharynx musculature or perhaps of the longitudinal muscles of the head which are adapted to the function of the protractile pharynx.

The pharynx sector following the fold, approximately 80 µ long (dph), is the only part of the foregut into which a large number of secretory ducts lead (Fig. 38, No. 63). The epithelium, while retaining its previous characteristic as skin epithelium, becomes lower here than in the fold. The pharynx wall itself consists not only of this epithelium but also of the mesenchyme layer containing the above mentioned secretory ducts and the 8 described longitudinal muscle fibres. Externally the pharynx, as all other sectors of the intestinal tract, is covered by splanchnic coelothelium (ct) which over the entire extent of the foregut has the same characteristics that were described for the somatic plate, i.e. a thin membrane with sparsely distributed nucleate protoplasmic proliferations (Fig. 38, No. 66 ct*). The secretory ducts quite evenly perforate the entire epithelium of this pharynx sector, and they belong to the above mentioned giant gland cells of the interior body mesenchyme. The route taken by the 4 clusters of secretory cells has already been described together with the head region, but this subject will be mentioned again below.

The remaining part of the foregut, the esophagus (Fig. 33, No. 1-4, oe), which extends as far as the 1st preclitellar somite, is of uniform structure over its entire length (Fig. 38, No. 63-67).

Inwardly its lumen is covered by an epithelium (oep) which, in keeping with the contractile state of the musculature in this sector of the digestive tract, either forms significant longitudinal folds (Fig. 38, No. 66) or - when these folds are flattened - has almost circular, smooth contours (Fig. 38, No. 64). The individual cells are of elongated shape, about 25-30 µ long and about 10-12 µ wide. Their cell body can be well distinguished from the adjacent elements on all sides ; facing the pharyngeal tube it has a seam which appears in cross section as a fine, sharply contoured line, similar to a cuticle.

Usually basally in the finely granulated, light-coloured protoplasm is the oval nucleus of about 10µ in length and 5-8 µ in width. It is not rich in chromatin and contains 1 or 2 nucleoli.

Resting directly against the epithelium is the thick circular muscle layer (rm) of the esophagus (Fig. 38, No. 63-67). Beginning at the posterior limit of the glandular pharynx sector with 2 or 3 poorly developed muscle cells (Fig. 38, No. 63), this layer then becomes very well developed and extends to the transitional point where the esophagus leads into the midgut. It consists of a single layer of muscle cells, each of which spans roughly half the cross section of the esophagus. The cells rest very closely against each other, and only in the most posterior part of the esophagus are they somewhat more sparsely distributed (Fig. 38, No. 65). In cross section each circular muscle cell is of oval shape, about 20-30µ in height and 15 µ in width. Toward the epithelium and on both sides the cells have a well developed fibrillar-contractile layer which is only absent on the outside, i.e. toward the coelom. Their finely granulated protoplasm stains quite well and contains an ovoid nucleus richly provided with chromatin granules, about 10µ in height and 8 µ in width; its longitudinal diameter reaches 20-

30 µ. The protoplasm is evenly and quite amply distributed over the entire length of the muscle cell; only at the ends is its circumference reduced by about half. As indicated above, the contractile-fibrillar layer fills the periphery of the muscle cell, but it is absent on its surface which faces outward, i.e. toward the coelom. Occasionally toward the cell ends this layer splits lengthwise into 2 strips, each of which is seen in section as an arc, giving the appearance of 2 muscle fibres connected by a common protoplasm. The protoplasm as well as the contractile-fibrillar layer have blunt ends. The nucleate sectors of the described cells touch each other lengthwise with the outer parts of their lateral surfaces, while extending between them inwardly, i.e. toward the epithelium, are the end sectors of those cells whose nuclei are situated at other points of the esophageal circumference.

Externally the circular muscles border on a thin mesenchyme layer (ms) which is covered toward the coelom by the above described coelothelium (ct, Fig. 38, No. 64-66).

Embedded in the mesenchyme layer are longitudinal muscle fibres (lm) which lie directly over the circular muscles (Fig. 38, No. 63-67). They represent a direct continuation of the longitudinal muscles in the wall of the glandular pharynx sector, and caudad they continuously merge into the wall of the midgut. In the entire periphery of the esophagus are about 12 such longitudinal muscle bundles, each formed by a single cell or by two cells. Each of these cells are only slightly longer than the somite in question; that is why each somite contains only one nucleus in each bundle, although no regularity can be observed in their distribution within the limits of each somite. As already indicated, the longitudinal muscle cells are of considerable length and insignificant thickness. The nucleate sectors form protoplasmic proliferations resembling a muscle body on which the contractile-fibrillar layer lies in the shape of a wide arc toward the epithelium. The ends of the muscle cells usually do not divide, and only occasionally do they split into 2 or 3 branches, in which case 2 or 3 muscle fibres extend to both sides from a single cell.

Attached to the esophagus are 4 pairs of protractors (pr_{1-4}) which are nothing but the dorsal dissepiment muscles already mentioned when the head region was described (Fig. 35, No. 18). It should only be added that when inserting in the esophagus, these muscle cells (pr_{1-2}) enter its mesenchyme layer where they divide into inconspicuous terminal branches (Fig. 38, No. 64, 66, 67).

Embedded in the mesenchyme of the esophagus, outwardly on each side anterior of the middle pair of protractors, are 1 or 2 circular muscle cells. These are very poorly developed elements with a dorsally situated nucleus, and they span only a small part of the esophageal circumference.

Also directly anterior of the two anterior pairs of protractors (pr_{1-2}) of the esophagus are circular muscle cells (mz) which in contrast to those above mentioned are very thick (Fig. 38, No. 63, 66, 67). Their beginning parts, which extend outwardly from the longitudinal muscles into the mesenchyme layer of the esophagus, are muscle fibres spanning about 3/4 of the periphery of the intestinal sector. Subsequently, wrapped in a thin mesenchyme layer, they detach from the wall of the foregut, forming a lamella (ml) situated outwardly of the latter which is covered on all sides with coelothelium (ct; Fig. 38, No. 66). These circular muscle fibres originate in 2 muscle cells whose nucleate sectors (mz) lie dorsally to the left and right in the described lamella (Fig. 38, No. 67). These cell sectors are extremely thick and of the same structure as the said dorsoventral muscles of the head region; almost their entire surface is covered with the contractile-fibrillar layer. Numerous processes extend dorsad and ventrad from the nucleate sector of such a cell, forming the circular muscle fibres of the lamella.

The 4 said secretory duct clusters (aup) of the giant gland cells pass the coelom, group themselves according to the 4 quadrants of the esophageal section, enter the mesenchyme of the lamella, squeeze through the muscle fibres, and extend further inward of the latter in the mesenchyme of the lamella (Fig. 38, No. 66).

Cephalad of the 1st pair of the circular muscle cells in the mesenchyme lamella lies the 2nd pair (mz) which is slightly smaller than the 1st pair but otherwise quite resembles it (Fig. 38, No. 67). The posterior muscle fibres of this pair directly border those of the 1st pair. The mesenchyme lamella containing them gradually approaches the esophageal wall with which it unites not far from the transition between esophagus and pharynx (Fig. 38, No. 63). The outer coelothelial layer of the lamella merges into the coelothelium which covers the foregut externally: the inner coelothelial layer, which covers the slit between the esophagus and the lamella in question, disappears together with this slit, and the mesenchyme of the lamella unites with the mesenchyme layer of the esophagus; the latter is also penetrated by the secretory ducts which are distributed evenly over the entire periphery of the esophagus and which then – in the pharyngeal wall – lead into the lumen of the pharynx.

Innervation of the foregut is supplied by nerves extending from 2 stomodeal ganglia (Fig. 38, No. 66, 67 sgn) embedded in the form of elongated oval masses of ganglia cells, one on each side, in the described mesenchyme lamella (ml) inward of their muscle fibres. The secretory duct clusters (aup) pass above and below the stomodeal ganglia. Cephalad, each of these ganglia extends one nerve which even in the mesenchyme lamella between the secretory ducts assumes a slightly ventral direction and detaches at the transition between the lamella and the intestinal wall. Here the nerve passes the narrow coelom sinus, then – ahead of the dorsoventral muscle cell of the 2nd head somite – enters the inner body mesenchyme, and unites with the nerve branch (n*) which arrives here, coming from the buccal cavity region (mh). The nerve formed by this union (n*) rises dorsad, curves around the outside of the dorsoventral muscle fibre (dvm_2) of the 2nd head somite, and finally enters the fibre mass of the pharyngeal connective; it is the 2nd nerve of the pharyngeal connective which was described above as the stomodeal nerve (Fig. 41, No. 101, 102).

In comparing the structure of the discussed intestinal sector of *Acanthobdella* and the corresponding intestinal sectors of the Rhynchobdellida, especially the Glossosiphonida, a common structural type can certainly be recognized. The proboscis sheath of the Glossosiphonida completely corresponds to the buccal cavity of *Acanthobdella*; they only differ in their relative dimensions. While the buccal cavity of *Acanthobdella* appears only as a rather inconspicuous invagination of the skin epithelium, the proboscis sheath of the Glossosiphonida is very well developed and extends caudad through a number of somites of the anterior body sector, in keeping with the extreme protractility of the proboscis. Yet in both cases the structural characteristics are almost the same. The wall of the proboscis sheath is formed on the inside by a flat epithelium that also has retained the character of regular skin epithelium, and on the coelom side it is covered with a thin mesenchyme layer traversed by longitudinal muscle fibres.

Furthermore, it is easy to find in the proboscis of Glossosiphonida the equivalent of all sections of the foregut of *Acanthobdella* The main difference between them is the degree in which the fold is developed. In *Acanthobdella* it is inconspicuous, in keeping with the poor development of the buccal cavity. It does not even reach the muscular esophagus and therefore appears as a simple pharyngeal fold. In the Glossosiphonida on the other hand, the fold together with the proboscis sheath is very well developed and reaches caudad almost to the posterior end of the muscular sector of the foregut. Actually this high degree of development of the fold is the only reason for the existence of the proboscis as a peculiar organ of the Rhynchobdellida.

A cross section through the middle proboscis sector shows a layer of elements on the inside which quite resemble the esophageal wall of *Acanthobdella* In the mesenchyme of the same a large number of secretory ducts is embedded over the entire periphery, while in *Acanthobdella* these are found only in the anterior sector of the esophagus. This layer of the proboscis is followed toward the outside by a second layer which forms the wall of the fold and whose structure is identical with the wall of the proboscis sheath, i.e. it represents a duplication of the latter. In *Protoclepsis tessellata* the author was able to find a reduction in the longitudinal muscle fibres in the esophageal proboscis wall where they persisted only in the posterior sector of the proboscis. However, the author has never observed that the secretory ducts are absent in the proboscis of this species, as claimed by R. LEUCKART (1894, p. 636).

A peculiarity in comparison with *Acanthobdella* is the presence of radial muscle fibres between the inner and outer epithelium layer in the proboscis of Rhynchobdellida. The Hirudinea may have inherited these fibres from their ancestors which were closely related to the Oligochaeta, since the radial musculature of the foregut is always present in the latter. In *Acanthobdella*, however, they have probably undergone a secondary retrogression.

Only in the extreme anterior sector of the proboscis is there a change in the described structure: here the circular muscle fibres disappear, and the secretory ducts open toward the outside. This part of the proboscis therefore completely resembles the pharynx of *Acanthobdella*, and this is also confirmed by the position at the anterior end of the fold.

Thus the proboscis of the Rhynchobdellida not only corresponds to the esophagus and pharynx of *Acanthobdella*, it is also in fact homologous to both of these together, since it was only the strong development of the fold in the buccal cavity that has transformed them into this peculiar, singular organ. However, it should be noted that the posterior sector of the esophagus does not participate in the formation of the proboscis, since the fold does not reach that far. That is why the mesenchyme layer here is without secretory ducts which diverge into the inner body mesenchyme at the margin of the cuff of the fold. This shows even more the similarity between the esophagus of the Glossosiphonida and that of *Acanthobdella*.

Therefore the discussed section of the intestinal tract of *Acanthobdella* can be regarded as being closely related to the type of foregut that should be considered as the early stage in the development of the buccal cavity and the proboscis of the Rhynchobdellida, and the same can be said about the glands of the foregut of *Acanthobdella*. As noted above, these glands are nothing but a special tract of the skin glands of the head region; at the same time they are without a doubt homologous to the salivary glands of the Rhynchobdellida. It can thus be stated that the glands of the foregut of *Acanthobdella*, which quite resemble the skin glands of the head and attachment disk region, are still in the undifferentiated state from which the salivary glands of the Rhynchobdellida - morphologically as well as physiologically sharply differentiated - have directly developed.

The innervation of the proboscis of the Rhynchobdellida also indicates relationships resembling the findings described for *Acanthobdella*. In both cases, two nerves are present, one on each side, originating in the pharyngeal connectives. In the proboscis or at the esophagus, respectively, they are provided with ganglial masses from which the further innervation of the various foregut sectors takes place. The only difference is in the route taken by the stomodeal sympathetic nerves, since in the Rhynchobdellida these must curve around the posterior section of the strongly developed proboscis sheath before entering the proboscis, while in *Acanthobdella* they do not require such a detour but enter the esophageal wall directly soon after originating in the pharyngeal connectives.

On the other hand, the structural nature of the foregut of *Acanthobdella* can very probably be regarded as very close to the original situation from which the development of this intestinal sector began in the Gnathobdellida, although in the latter it is subject to far more important changes than in the Rhynchobdellida. The small buccal cavity of *Acanthobdella* has become much larger in the Gnathobdellida where it extends through several head somites, which is also the case in the Rhynchobdellida. However, this is not a fundamental difference. The structure of the long, strongly developed esophagus of the Gnathobdellida provides the most unambiguous indication that this organ is directly homologous in *Acanthobdella* and the Rhynchobdellida, while all deviations are obviously caused by the reduction of the coelom and the resulting new relationships between the muscle layers. In Gnathobdellida, the pharynx characterized by the endings of secretory ducts shows the most significant changes in comparison with the *Acanthobdella* type: it has either disappeared as in the Herpobdella, or it has developed into the jaw apparatus lying between the buccal cavity and the esophagus, i.e. at the place originally assigned to the pharynx. Apparently the fold of the anterior pharynx sector of Acanthobdella is of roughly the same structure in the Gnathobdellida where it forms a sort of buccal cavity pockets which posteriorly border on the jaws. In keeping with the development of the mesenchyme in the Gnathobdellida, the glands and their secretory ducts have retreated from the esophageal wall into this body layer. Thus the most significant difference in comparison with the Rhynchobdellida is the absence of a more significant duplication of the buccal cavity wall which in the latter has led to the formation of the proboscis sheath and the outer wall of the proboscis. Also connected with the above noted changes in the overall foregut structure are changes in the sympathetic nervous system of the Gnathobdellida which – in addition to the ganglia adjacent to the two pharyngeal connectives which are strictly homologous to the sympathetic stomodeal ganglion accumulations in Rhynchobdellida and *Acanthobdella* – has developed other, purely local ganglial formations.

It thus follows that the anterior intestinal sector of the Gnathobdellida shows no fundamental differences in comparison with *Acanthobdella*, rather its structure has quite clearly pronounced homologies with the corresponding intestinal sector in *Acanthobdella*, which represents a situation very close to the original state which must have given rise to the development of the foregut in the Gnathobdellida.

Finally some comments are in order about the views expressed by R. LEUCKART (1894) regarding the anterior intestinal sector of the Hirudinea. LEUCKART's description differs very significantly from the present author's in terms of the nomenclature of the anterior sectors of the foregut, and especially as far as the homologization of the two main groups of Hirudinea are concerned. Thus he wrote on p. 612: "If one interprets the proboscis as the pharynx, as is usually done, and then compares it with the structure of the same name in the Gnathobdellida [the esophagus according to the present author's nomenclature], the development is highly conspicuous. It would mean that the pharynx has shifted into the buccal cavity itself. But is the proboscis of the Rhynchobdellida really morphologically homologous to the pharynx of the Gnathobdellida?" LEUCKART further questions this homology and thinks that the proboscis "should more appropriately be equated to the jaw apparatus which also protrudes into the buccal cavity – only not as high". LEUCKART continues: "Such an interpretation would also easily explain the tube leading to the chylus stomach, which is lacking in the Gnathobdellida, but almost as typical for the Rhynchobdellida than the proboscis itself: it would become the pharynx". His own words indicate that LEUCKART is trying to divide the indivisible (p. 643): "The connection between these two structures" [i.e. his proboscis and pharynx] "is still more complete than it seems at first glance". And indeed these structures – the oesophagus sector included in the proboscis and that situated behind the proboscis – do not differ from each other except that resting against the former is an epithelium fold, while the latter is lacking such a duplication. If LEUCKART's division proves to be artificial, his statement on p. 643 also becomes invalid: "Functional changes make it understandable that the structure of the proboscis often resembles the pharynx of the

Gnathobdellida, at first glance justifying a parellelization of both structures". However, in this case, as we have seen, the resemblance means a true homology, and it is unnecessary to cite "functional changes" to explain the facts. At the same time, of course, the fantastic assumption (p. 638) that "the 3 jaw bulges of the latter" [i.e. the Gnathobdellida] "are elongated, growing together with their margins to form a tube" is thus automatically eliminated.

As far as the structure of the foregut is concerned, the relationships between the Oligochaeta and *Acanthobdella* are much less distinct than those between *Acanthobdella* and the other Hirudinea. The same structure type, already very much modified, is apparent in the anterior intestinal sector of *Branchiobdella* However, as far as the author knows, *Haplotaxis* is the only typical Oligochaete whose characteristics in this intestinal sector resemble – or, more accurately, apparently resemble – those of *Acanthobdella*, which with a certain degree of probability can be regarded as being close to the primitive state and as the origin of the development of the apparatus found in *Acanthobdella*

In the mid sector of the 1st preclitellar somite (6) of *Acanthobdella*, the esophagus (oe) quickly narrows and merges into the midgut (d; syn.: crop, chylus stomach in the other Hirudinea; Fig. 33, No. 1; Fig. 41, No. 106). Although no sphincter is present at this point, and although on the contrary, the circular musculature (rm) of the esophagus is reduced here and its last fibres are very poorly developed (Fig. 38, NO. 65), the esophageal tube corresponds with the lumen of the midgut through a very narrow opening.

Beginning in the 1st preclitellar somite (6), the midgut (d) of *Acanthobdella* extends through 13 body somites and thus constitutes the largest portion of the intestinal tract (Fig. 33, No. 1), 5, 6; Fig. 34, No. 7-

11). In the beginning the midgut is a rather narrow tube, but later it gradually widens (Fig. 41, No. 106) until it almost entirely fills the coelom sinus in the mid body somites (Fig. 34, No. 10). In the clitellar somites the described intestinal sector is somewhat narrower to make room for the various parts of the sexual apparatus (Fig. 33, No. 6; Fig. 34, No. 7-9). In the region of the dissepiments very slight constrictions of the midgut can also be observed (Fig. 34, No. 11). It should be noted that this ordinary, " normal" appearance can be subject to quite significant changes, depending mainly on the amount of food in the intestinal lumen.

The midgut of *Acanthobdella* is usually filled with the blood of the host, as A. KOWALEVSKY (1896) also reported. However, the blood corpuscles even in this sector of the intestinal tract show little or no discernable changes, so that actually the midgut serves only as a reservoir for this component of the absorbed blood before it is transported further into the hindgut. In this respect, the midgut of *Acanthobdella* shows a certain analogy to that in the other Hirudinea.

The epithelium (dep) of the midgut (Fig. 36, No. 36, 37; Fig. 37, No. 38-40; Fig. 38, No. 68; Fig. 39, No. 83-85) forms only inconspicuous longitudinal folds in the widened parts of the midgut. In the most anterior parts however, where the midgut becomes gradually narrower, the longitudinal folds are more pronounced, depending on the degree of narrowing. In the dissepiment regions where the midgut is constricted, the epithelium layer also has folds which, however, run laterally and are quite inconspicuous (Fig. 37, No. 39).

Low, almost cubic epithelium measuring about 10-12 µ in height is found between the folds over large parts of the midgut (Fig. 36, No. 36). When folds are formed, the cells become significantly higher and narrower,

318

and their proximal parts thicken and become club-shaped (Fig. 36, No. 37; Fig. 37, No. 38-40). The protoplasm of the epithelial cells is of finely granulated appearance and contains a large number of vacuoles, usually of insignificant size. Proximally these vacuoles are absent in the cells, and here the protoplasm is very finely striated at the margin (Fig. 38, No. 68). The epithelium may actually be very finely ciliated, as is the case in the major portion of the intestine in Oligochaeta, and as some authors have described it in the Hirudinea as well. In *Acanthobdella*, the nuclei are situated basally or in the middle of the epithelial cells; they are either spherical, with a diameter of about 7 µ, or oval. They contain only few chromatin granules and usually only one nucleolus.

Between the basal sectors of the epithelial cells, sparse ganglion cells belonging to the sympathetic nerve plexus are embedded. These cells are irregular in shape, stain very well, have a finely granulated protoplasm and a large, light-coloured nucleus. The latter is 2-3 times as large as in the adjacent epithelial cells and contains a significant number of chromatin granules of various sizes.

Resting against the epithelium externally is the layer of intestinal mesenchyme (ms) which in turn is covered by the described chloragogen cells (clz) and coelothelial muscle cells (Fig. 36, No. 36, 37; Fig. 37, No. 38-40; Fig. 38, No. 68).

The mesenchyme layer (ms) of the midgut is very thin and consists of a transparent, gelatinous substance in which very rarely some cellular elements, resembling the amoebocytes of the inner body mesenchyme, are encountered. Distad, i.e. toward the coelothelium, as well as proximad, i.e. toward the intestinal epithelium, the mesenchyme secretes very thin but clearly defined marginal lamellae. Cephalad the mesenchyme layer of the midgut directly merges into that of the esophagus, and the logitudinal muscle fibres (lm) of the latter also continue into the midgut (Fig. 36, No. 36; Fig. 47, No. 38, 40; Fig. 39, No. 83-85). Here these fibres (lm) assume a much more regular course in the mesenchyme layer than in the described foregut sections: their nucleate cell sectors are almost always situated near the anterior somite margin. As a rule, the said longitudinal folds of the midgut epithelium assume the same course as these longitudinal muscle fibres. Each somit contains roughly up to 12 muscle cells, although this number can be higher or lower. Occasionally the muscle fibres of a given somite deviate from the corresponding fibres of the adjacent somite over a certain length of the intestinal circumference, and this circumstance causes an apparent increase in the overall number of longitudinal muscle fibres; for the same reason, the number of longitudinal folds of the intestinal epithelium may change, too. In that case the muscle fibres themselves are very thin and very small in section. Their protoplasm expands only over an insignificant distance toward both sides of the nucleate sector, while the cells reach a length of about 1 1/2 somite lengths. The nucleate protoplasm accumulations (lm*) are covered by the contractile-fibrillar layer only on the surface facing the epithelium, on which the layer occupies no more than half the space. However, occasionally the longitudinal muscle fibres divide lengthwise, although it is seldom that 2 separate fibres of the contractile-fibrillar substance already occur in the nucleate cell sector (Fig. 37, No. 38).

As described above, the circular muscle layer (rm) of the midgut (Fig. 36, No. 37); Fig. 37, No. 38-40) is formed by coelothelial muscle cells (Fig. 36, No. 37; Fig. 37, No. 38, rm*), and the muscle fibres in question extend distad, i.e. toward the coelom, from the outer marginal lamella of the mesenchyme layer (ms). In each somite, namely in its most anterior sector, the dissepiment contains 2 circular muscle cells (rm*) on each side, which are entirely embedded in the mesenchyme layer (Fig. 37, No. 39, 40). Their origin from ordinary coelothelial cells has been discussed above, and it should only be mentioned here that the muscle ring formed by these cells, together with the dissepiment muscle cells, causes the ring-shaped constrictions of the midgut.

At the end of this description of the midgut of *Acanthobdella*, the author wishes to discuss some physiological facts concerning this intestinal sector.

As mentioned above, the cells of the midgut epithelium contain numerous vacuoles. These vacuoles are filled with droplets of a substance that becomes a deep black when stained with osmium (Fig. 38, No. 68). With other methods, the substance dissolves, and then only colourless vacuoles are visible in the protoplasm of the cells. In a midgut section stained with osmium, the middle and basal sectors of the epithelial cells are very densely packed with the said black droplets, and only the nucleus forms a light oval between them (Fig. 38, No. 68). Toward the proximal periphery of the cells the number and size of these black droplets decreases, while the marginal layer of the protoplasm is entirely without them. The same black droplets can be seen in the mesenchyme layer (ms) of the midgut, albeit in considerably smaller numbers than in the epithelial cells. The basal and middle sectors of the chloragogen cells (clz) also contain such droplets, but distally in the cells they occur only in very small numbers or not at all. The question is how to interpret this phenomenon. The author feels that undoubtedly these droplets consist of some fat-like substance, that they accumulate on one side in the epithelial cells of the midgut, on the other side in the chloragogen cells, and that they then pass the thin intestinal mesenchyme and migrate from one cell layer to the other.

The direction in which this migration must take place will depend on the physiological process taking place here, which in this case probably consists of digesting the nutrients contained in the intestine. In other words, this would mean that the fat-like droplets pass from the epithelial cells of the midgut through the mesenchyme layer to be absorbed by the chloragogen cells. Migration in the opposite direction is not very likely, since it could only take place with extremely intensive excretory activity of the chloragogen cells and the midgut epithelium, which seems almost paradoxical.

Naturally this raises an additional question: which part of the absorbed blood would be processed in the manner described, since the blood corpuscles pass the midgut almost unchanged? The answer is very simple: it is apparently the other component of the blood, namely the blood plasm. The latter or some conversion product of the same leaves the intestine and enters the protoplasm of the epithelial cells where conversion into a fat-like substance occurs. That such a process must indeed take place in the protoplasm of the epithelial cell is indicated by the fact that the proximal cell sector contains no droplets of the fat-like substance, while the middle and basal sectors are densely packed with them. The droplets move unchanged from the epithelial cells through the mesenchyme layer into the chloragogen cells, where they are apparently again converted before their substance merges with or is assimilated by the coelom fluid. This assumption is based on the circumstance that free cells containing droplets of the fat-like substance occur very rarely in the coelom, and that free droplets never occur. This also finally explains why the fat-like droplets are found mainly in the basal and middle sectors of the chloragogen cells, while they disappear toward the distal end of the cells.

Thus we have a rather certain indication of one aspect of the activity of the chloragogen cells, namely their participation in the organism's nutrition process. This has been noted by several authors who have specifically examined the chloragogen tissue. The present author wishes to cite only the following words by G. SCHNEIDER (1896, p. 386): "... the chloragogen cells ... regulate nutrition ... and are thus most likely depositories for reserve food which they 'draw' from the blood lacunae of the intestinal wall and from the blood vessels to which they are attached". It should be added that they also "draw" directly from the intestinal mesenchyme. W. RICE (1902) in his most recent studies of chloragogen cells attributed an originally assimilatory function to them. C. BERTOLOTTI (1902) regarded them as elements which also serve as depositories for reserve material.

Anteriorly of the dissepiment between the 8th mid body somite (19) and the 1st somite of the hindgut region (20) the midgut suddenly narrows (Fig. 33, No. 1; Fig. 41, No. 108) and subsequently merges into the following sector of the intestinal tract, namely the hindgut (hd) which in the other Hirudinea is called entodermal hindgut, intestine, or endgut. The opening leading from the midgut to the hindgut has a very small diameter. Immediately behind this constriction, the hindgut widens in the 1st somite (20) of the hindgut region, almost completely filling this coelom sector (c_{20}; Fig. 34, No. 12; Fig. 41, No. 107, 108). In the dissepiment (dsp_{20}) between the 1st and 2nd somite of the hindgut region, and in the following 3 dissepiments (dsp_{21}, dsp_{22}, dsp_{23}), i.e. between the 2nd and 3rd, 3rd and 4th, 4th and 5th somites of this region, the hindgut has constrictions that are almost as deep and sharply defined as those at the boundary between midgut and hindgut. The widened sectors of the hindgut (hd_2, hd_3) situated in the coelom sinuses (c_{21}, c_{22}) of the 2nd (21) and 3rd (22) somite are smaller than in the 1st somite. Even less developed is the sector (hd_4) situated in the coelom sinus (c_{23}) of the 4th somite (23). In the coelom sinus (c_{24}) of the 5th somite (24) the hindgut again widens quite considerably and continues as a wide tube (hd_5, hd_6) up to the point where it leaves the coelom and enters the inner body mesenchyme behind the last dissepiment (dsp_{25}); the constriction between the 5th and 6th somite (25) and behind the 6th somite of the hindgut region, is very insignificant.

Thus the entire hindgut can be divided into 2 parts, the anterior of which has 4 well-formed, expanded sectors (hd_{1-4}) with well-defined constrictions between them, while the posterior part ($hd_{5,6}$) forms a uniformly wide tube over its entire length (Fig. 41, No. 107, 108). This characteristic very much resembles the situation found in the Glossosiphonida and the Hirudinea in general. Thus the structure of the hindgut of *Acanthobdella* represents a transitional stage between the undifferentiated state in the Oligochaete intestine and the relatively highly developed type in the Hirudinea, which is certainly to be regarded as an adaptation to the latter's specific habits.

While the connection between midgut and hindgut is situated in the lateral plane of the body and on its longitudinal axis, the constrictions between the 4 widened hindgut sectors are not nearly as regularly oriented. These constrictions usually lie off the longitudinal axis of the body and form a more or less pronounced angle together with the transverse plane (Fig. 41, No. 107). Accordingly one side in the widened sections of the hindgut, namely the side into which the previous constriction of the sector deviates from the longitudinal body axis, is far more developed than the opposite side. In other words, the hindgut forms creases in the first 4 somites of its region, and this circumstance together with the deep constrictions makes it possible for the intestinal sectors (hd_{1-4}), which belong to the 4 anterior somites (20-23) of the hindgut region, to find room over an area of about 2 somites (20, 21). The reason for such a displacement may be that the anal opening has shifted forward by several somites. As described above, the forward shift of the dissepiments of the coelom corresponding to the constrictions of the hindgut, and thus, of course, also of the corresponding somite sinuses, has to be regarded as the result of the same process. However, in view of the development of the attachment disk and its musculature, the change in position of the anus was inevitable if this opening was to retain its ability to function.

Over the whole length of the hindgut, the lumen is lined with an entirely uniform epithelium layer (dep; Fig. 34, No. 12, 13; Fig. 38, No. 70; Fig. 39, No. 71), whose cells can be quite well distinguished from those of the midgut. They are ordinary cylindrical cells which are about 20 µ long and 6 µ wide in the widened sectors of the hindgut. In the 10-12 longitudinal folds and at the constrictions, the epithelium reaches a length of about 40-50 µ; the cells are basally somewhat narrowed, distally thickened, although occasionally they are of uniform width over their entire length. The nucleus in the middle sector of the cell body is of spherical or more often oval shape, about 8-10 µ in length and 5-6 µ in width. It is more amply provided with chromatin granules than in the epithelial cells of the midgut, and it usually contains 1 or 2 nucleoli. The protoplasm of these epithelial cells is quite uniformly finely-grained and itself vacuolized only

76.8

at the margin (Fig. 39, No. 71); in the mid sector it contains numerous vacuoles whose number gradually decreases basally. Basally the protoplasm is more evenly distributed, since only very few vacuoles are present here. All vacuoles except those found peripherally toward the inside contain droplets of the fat-like substance that was described in terms of the epithelial cells of the midgut. They turn a very deep black when stained with osmium (Fig. 38, No. 59, 70).

Between the basal sectors of the epithelial cells sparsely distributed ganglion cells of the sympathetic intestinal plexus are encountered which do not differ from those of the midgut except that they seem to occur in greater number in the hindgut.

The mesenchyme layer resting against the epithelium from the outside represents a direct continuation of the same layer in the midgut, and its peritoneal sheath (ct) is similarly formed of chloragogen (clz) and coelothelial cells (Fig. 39, No. 71). The circular muscle fibres originating in the latter form the entire circular musculature of the hindgut.

One peculiarity of this intestinal sector is that its mesenchyme layer contains cavities (ds which hold blood and which are in open contact with the dorsal (dg) and ventral (vg) blood vessel (Fig. 34, No. 12; Fig. 39, No. 71). These cavities are distributed over the entire hindgut (Fig. 41, No. 108); they have no walls of their own and are surrounded on all sides by the intestinal mesenchyme. The latter divides here into 2 thin lamellae, the inner of which is resting against the epithelium of the hindgut, the outer against its coelothelium. Between the two lamellae, thin mesenchyme strands (ms) are often present which connect the lamellae (Fig. 39, No. 71). As in the midgut, the mesenchyme itself consists of a transparent, gelatinous substance with almost no cells.

The longitudinal muscle fibres (lm) continue directly from the midgut to the hindgut where they are resting inside against the outer mesenchyme lamella, surrounded by a thin layer of the mesenchyme (Fig. 34, No. 12; Fig. 39, No. 71). On the edge of each intestinal sector corresponding to a somite, the nucleate protoplasm proliferations are seen which belong to the longitudinal fibres. This arrangement is highly regular and consistent and appears to be a significant characteristic of the relevant sectors of the hindgut somites. 10 or 12 of these nucleate protoplasm proliferations of the longitudinal muscle fibres are found in all dissepiments of the hindgut region, even in the last, poorly developed body dissepiment. This confirms that the latter structure is indeed a dissepiment.

Above these 10-12 longitudinal muscle fibres of the hindgut the longitudinal folds of the epithelium are forming. The latter are more developed than in the midgut, and they contain quite sizeable longitudinal cavities which represent the widest and most spacious sectors of the intestinal blood sinus (Fig. 39, No. 71).

Externally, the circular muscle layer of the hindgut coming from the coelothelial muscle cells is resting against the marginal lamella of the mesenchyme layer. Only in the posterior sector of each somite, directly behind the corresponding dissepiment or almost in the latter itself, 2 circular muscle cells occur on each side which are entirely embedded in the mesenchyme layer. In the last body dissepiment these muscle rings are no longer present.

Thus the musculature of the hindgut has exactly the same relationships as that of the midgut.

In the other Hirudinea the musculature of the entodermal intestinal section has similar characteristics as in *Acanthobdella*, and the present author can only confirm what LEUCKART (1894, p. 661) wrote about this. However, *Acanthobdella* is most closely related to that group of Oligochaeta in whom – as the author has described elsewhere (LIVANOW, 1904, 1) – the circular muscles are situated outwardly, i.e. toward the coelom, in relation to the longitudinal muscles, namely *Branchiobdella* and *Haplotaxis*. In terms of their intestinal musculature these species are fully identical to *Acanthobdella*, while in the other Hirudinea – because of the extreme development of the mesenchyme and the almost total disappearance of the coelom sector surrounding the intestine – the coelothelial muscle cells have been replaced by true muscle cells. This is also the reason why the Hirudinea are without the chloragogen cell layer which is typical for the Oligochaeta and which is still present in its entirety in *Acanthobdella*.

While the above facts show that *Acanthobdella* is closely related to the Oligochaeta, the entodermal intestinal sector of this species shows on the other hand that in all other respects *Acanthobdella* undoubtedly belongs to the Hirudinean type. This becomes most apparent in the division of the entodermal intestine into 2 sectors, namely the midgut and hindgut. In Oligochaeta no such intestinal division can be made, and its development in the Hirudinea should probably be attributed to their specialized parasitic mode of feeding. Now a few remarks about the function of the hindgut of *Acanthobdella*.

As A. KOWALEWSKI (1896) already noted, the absorbed blood corpuscles which remain almost unchanged in the anterior sectors of the digestive tract, are broken down in the hindgut. This circumstance indicates with certainty that the food is subjected to an enzymatic digestive process in the hindgut, probably facilitated by the secretion that gives the vacuolized appearance to the proximal ends of the epithelial cells.

On the other hand, there can also be no doubt that assimilation processes take place in the epithelial cells of the hindgut. As mentioned above, over the entire length of the hindgut these cells contain droplets of a fat-like substance that stains very well with osmic acid. This shows that initially the fat droplets collect in small numbers in the mid sector of the cell body proximally of the nucleus (Fig. 38, No. 70). Later they also appear basally of the nucleus (Fig. 38, No. 69), and occasionally the entire mid sector of the cell right around the nucleus is filled with fat droplets resting closely against each other. The proximal sector always remains without these droplets. This indicates that the food material entering from the intestinal lumen is probably converted into a fatty substance in the cell body, even in the vicinity of the nucleus.

Then the droplets migrate from the mid sector to the basal cell sector where they are already found in relatively small numbers. From here they apparently advance through the bars of the mesenchyme layer to the chloragogen cells in which the fat-like droplets again accumulate in large numbers (Fig. 38, No. 70). The latter process is quite similar to that described above for the midgut.

However, there is as yet no answer to the following question: what conversion products of the blood contained in the intestinal tube of *Acanthobdella* are assimilated here, especially since other, less conspicuous processes than those described may take place in the hindgut?

Even though it can be assumed from the facts discussed above that the assimilation processes in both sectors of the entodermal intestine are similar to some degree, there can be no doubt on the other hand that digestion of the blood corpuscles is characteristic only for the hindgut. This is also confirmed by the said peculiarities of its epithelium. Perhaps it is connected with the presence of a blood sinus in the hindgut alone, while such a sinus is lacking in the midgut.

The same peculiarities characterize the two sectors of the entodermal intestine in the other Hirudinea, in contrast to the Oligochaeta. The glandular epithelium as well as the blood sinus always occur in the hindgut of the latter, while there is no blood sinus in the midgut, and the epithelium loses its glandular character.

As mentioned, the hindgut of *Acanthobdella* can be said to represent the preliminary stage to its further differentiation into 2 sectors, a condition very well developed in many Hirudinea. This is confirmed, for example, by the fact that the functions of both sectors are identical in *Acanthobdella* and the other Hirudinea, and by the identical relationships with the blood sinuses. The illustrations and descriptions of A. OKA (1894) concerning the blood sinus of *Hemiclepsis marginata* and other Glossosiphonida apply almost entirely to *Acanthobdella* as well.

Directly behind the last body dissepiment, the hindgut of *Acanthobdella* enters the inner body mesenchyme (Fig. 34, No. 13; Fig. 41, No. 108). The coelothelium leaves the hindgut here, its mesenchyme layer merges with the inner body mesenchyme, the cavities containing blood disappear, and the longitudinal muscle fibres end. The rather wide intestinal tube quickly narrows, and the hindgut (hd) changes into the short end gut (an), which rises vertically dorsad, perforates the musculature of the body wall and opens to the outside between the 4th (23) and 5th (24) somite of the hindgut region through a narrow slit lying on the dorsal median line, transversely to the longitudinal body axis.

The epithelium lining the end gut represents a direct continuation of the skin epithelium, and its structure does not change at all over the short distance from the hindgut to the anal opening (Fig. 31, No. 13). The cells are identical to those of the skin epithelium; their cuticular seam is well developed. At the transition from end gut to hindgut a sharp border can be seen between the cells of the two intestinal sectors, which makes it possible to ascertain the ectodermal origin of the end gut.

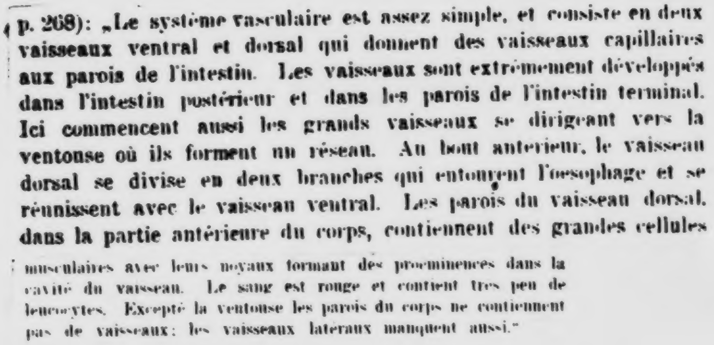
Its musculature is sharply delineated from the said musculature of the entodermal intestinal section (Fig. 34, No. 13). Resting against the epithelium are well-developed circular muscles whose number totals about 10 bundles. Cephalad they extend slightly into the hindgut, while caudad they follow directly the circular musculature of the integument from which they cannot be distinguished.

Distally of the circular muscles are a few poorly developed longitudinal muscle fibres whose terminal rami on the one side attach themselves between the circular muscles of the integument and on the other side reach as far as the hindgut. Their nucleate sectors are at the dorsal part of the endgut, and the general structure of these cells cannot be distinguished from that of the circular muscles.

Summarizing the findings in regard to the intestinal structure of *Acanthobdella*, it can be stated that the intestine of this species is definitely true to Hirudinean type, but of a primitive state that is very closely related to the Oligochaete type, especially to that in species such as the Haplotaxida and *Branchiobdella*

11. The blood-vascular system

A. KOWALEWSKY wrote as follows about this system (1896, p. 268):



(p. 268): „Le système vasculaire est assez simple, et consiste en deux vaisseaux ventral et dorsal qui donnent des vaisseaux capillaires aux parois de l'intestin. Les vaisseaux sont extrêmement développés dans l'intestin postérieur et dans les parois de l'intestin terminal. Ici commencent aussi les grands vaisseaux se dirigeant vers la ventouse où ils forment un réseau. Au bout anterieur, le vaisseau dorsal se divise en deux branches qui entourent l'oesophage et se réunissent avec le vaisseau ventral. Les parois du vaisseau dorsal, dans la partie antérieure du corps, contiennent des grandes cellules musculaires avec leurs noyaux formant des proéminences dans la cavité du vaisseau. Le sang est rouge et contient tres peu de leucocytes. Excepté la ventouse les parois du corps ne contiennent pas de vaisseaux: les vaisseaux lateraux manquent aussi."

E. GRUBE (1851) wrote only that he could "recognize fragments of one of the lateral vessels, but could not fully understand its connections".

The most important components of the well-developed and well-defined blood-vascular system of *Acanthobdella* are the ventral (vg) and dorsal (dg) blood vessels which in the greater part of the body, from the head region to the hindgut region, are the only blood vessels present (Fig. 33, No. 3-6; Fig. 34, No. 7-12; Fig. 41, No. 108); longitudinal secondary blood vessels do not occur at all.

The ventral blood vessel (Fig. 33, No. 3-6); Fig. 34, No. 7-13; Fig. 40, No. 92; Fig. 41, No. 108 vg) extends in the ventral coelom sector along the median line of the body, above or beside the ventral cord. The ventral vessel shows no traces of a ventral part of the vascular mesentery, while traces of the dorsal part are always present. It can be seen that in the dissepiments of all somites in the mid body and hindgut regions the ventral blood vessel is connected to the intestinal mesenchyme by a mesenchymatous strand which, as all formations in the coelom, is covered on the outside by ordinary coelothelium (Fig. 34, No. 11; Fig. 41, No. 108). 1 or 2 muscle fibres traverse this strand as far as the vessel itself. These are the terminal rami of the smaller pair of muscle cells (dsz_1) which extend ventrally to the intestine in the dissepiment. In the clitellar and preclitellar somites the mesenchyme strands are sometimes present, sometimes not. In some cases the author found that the dorsal part of the ventral mesentery occasionally occurs in the preclitellar somites as a thin mesenchyme lamella over a varying distance. In the 1st clitellar somite such a mesenchyme lamella connects the ventral blood vessel with the dorsal wall of the ventral coelom sinus, or the vessel is completely enclosed in that wall (Fig. 34, No. 8). In the head somites the ventral blood vessel has no remnants of the mesentery. (Fig. 33, No. 2-4).

From the 1st preclitellar somite (6) to the attachment disk region the ventral blood vessel is quite uniform (Fig. 39, No. 72; Fig. 40, No. 92). Its oval or round cross section has a diameter of about 20-25 μ. Under its coelothelial coating (ct) lies a thin layer formed by ordinary transparent gelatinous mesenchyme (ms) with very sparsely distributed cells. Inwardly this layer provides a very well-developed marginal lamella which becomes distinctly red when stained after Van Gieson (hematoxylin/acid fuchsine/picric acid). It is bordered by the inner layer (is) of the vessel wall which does not stain red. The wall is formed by a very thin protoplasmic lamella in which are embedded 5-6 non-ramified lateral muscle filaments (mf) of round or oval cross-section. The inner surface of this protoplasmic lamella, facing the blood vessel lumen, has a strongly light-refractory cuticular seam which, however, does not constitute a special membrane that could be compared to an intima. In some places the protoplasm seems to be entirely absent in this cuticula, while in other places it forms proliferations (is*) which reach into the blood vessel lumen, taking up almost 1/3 of its space (Fig. 39, No. 72b). Here the finely granulated protoplasm, which stains well, shows a relatively large oval nucleus about 10 μ in diameter, with small chromatic granules. At the inner margin the said longitudinal muscle filaments extend inside the protoplasm proliferation. The proliferations usually occur in pairs in each somite, but no regularity can be observed in their arrangement apart from the fact that they are distributed biserially to the left and right in the blood vessel wall.

Other cell elements cannot be found in the inner wall layer of the ventral blood vessel. The cells must therefore be those which form the inner wall of the blood vessel and at the same time represent the cells from which the musculature of the wall originates, namely the longitudinal muscle filaments.

In the Glossosiphonida the ventral blood vessel shows quite the same structure. The only difference is that here the inner layer of the vessel is very thin and can very easily be overlooked.

As far as the literature on the ventral blood vessel of the Glossosiphonida is concerned, reference is made to the summary provided by A LANG (1903, p. 253-259), since the present author fully agrees with LANG's evaluation of the available material. It should only be added that the present author still maintains that the longitudinal muscle filaments in the ventral blood vessel wall which he described do indeed exist, and that in this regard he cannot agree by any means with LANG's interpretation that they are folds of the inner layer. The present author believes that as far as can be determined from the writings of several authors, this should be regarded as a difference between the Hirudinea and the Oligochaeta.

In the head region as well as in the attachment disk region, the structural characteristics of the ventral blood vessel change. Typically the ventral vessel extends, as described above, cephalad to the dissepiment of the 5th head somite and the 1st preclitellar somite. When it reaches the ventral point of penetration of this dissepiment, the ventral blood vessel (vg) gives off a pair of transverse vessels (Fig. 33, No. 4, gg; Fig. 41, No. 103, qg_5). Two of the longitudinal muscle filaments of its wall (one on each side) disappear by ending here or perhaps merging with the corresponding transverse vessels. However, if the latter should be the case here, only the end of the filament would enter the wall of the transverse vessel.√In the dissepiment between the 4th and 5th head somite the vessel again gives off a pair of transverse vessels (qg_1; Fig. 41, No. 103); again two longitudinal muscle filaments of its wall come to an end here. Thus only 1-2 longitudinal muscle filaments remain in the ventral blood vessel, which also disappears at the dissepiment between the 3rd and 4th head somite, where the 3rd pair of transverse vessels (qg_3) is given off by the ventral blood vessel.

This regularity in the gradual disappearance of the muscle filaments is usually very pronounced, but occasionally some extra filaments can be found, or the ordinary filaments may continue beyond the normal point.

At the boundary between the 2nd and 3rd head somite the ventral blood vessel gives off another 2 transverse vessels (qg_2), the 4th pair, and continues between the esophagus and the subesophageal ganglion mass,

In the 5th head somite the ventral blood vessel has only 3-4 longitudinal muscle filaments.

after which it divides into its 2 anterior terminal branches (Fig. 33, No. 2 vg; Fig. 39, No. 2 vg; Fig. 39, No. 73; Fig. 41, No. 103 qg_4).

Caudad the ventral blood vessel retains its ordinary structure until it enters the posterior pouch-like terminal part of the coelom where it approaches the anal ganglion mass (Fig. 41, No. 108). While it is dorsally resting against this part of the ventral cord, it gives off 3 pairs of transverse vessels during its further path (Fig. 41, No. 104 qg_{1-3}). These transverse vessels pass between the lateral clusters close to the central fibre mass, in ventral and slightly lateral direction. The anterior pair (qg_1) is situated between the 1st and 2nd ganglion complex of the anal ganglion mass, the following pair (qg_2) between the 2nd and 3rd, and the 3rd pair (qg_3) between the 3rd and 4th ganglion complex.

Directly behind the anal ganglion mass the ventral blood vessel again gives off 1 pair of transverse vessels (qg_4), one or the other of which occasionally remains united with the longitudinal vessel for a certain distance, which can more or less obscure the typical characteristics.

Ahead of or slightly behind the most anterior pair of transverse blood vessels the longitudinal muscle filaments disappear in the most posterior part of the ventral blood vessel, and the structure of the latter is very similar here to that in the said anterior sector. Under its outer coelothelial coating it has a thin mesenchyme layer where in the region of the anal ganglion mass some gland cells and their secretory glands leading toward the attachment disk can be observed (Fig. 34, No. 13). It also has an inner layer whose cells are formed as usual but do not contain the muscle filaments.

Structurally the transverse blood vessels cannot be distinguished at all from the muscle-less parts of the ventral blood vessel, except for their smaller size (Fig. 39, No. 74, 75).

The same applies to the structure of the transverse blood vessels in the Glossophonida.

The small vessels connecting the ventral blood vessel with the said intestinal blood sinus (Fig. 41, No. 108) have a different structure. There are 5 of these, and they extend inside the mesenchyme membranes that suspend the ventral blood vessel at the intestine between the 1st and 2nd, 2nd and 3rd, 3rd and 4th, 4th and 5th, 5th and 6th somites of the hindgut region. Since they are provided with muscle filaments, their structure generally resembles that of the ventral blood vessel. In their walls they contain 2-3 or more cells, depending on the length of the vessels, and the cells are provided with 2-3 longitudinal muscle filaments. The latter end on one side in the outer mesenchyme lamella of the hindgut wall where the vessel enters the sinus, and on the other side where the vessel joins the ventral blood vessel. The vessels are formed exclusively by these cells and have no other layers, since they are surrounded on all sides by the mesenchyme of the suspension membrane.

According to observations by the author and by OKA (1894) such vessels do not exist in the Glossosiphonida, while such anastomoses do occur in the Oligochaeta between the ventral blood vessel and the intestinal blood sinus.

The dorsal blood vessel (dg) runs in the dorsal coelom sector above the intestinal tract parallel to the ventral coelom sector. Where there are ovisacs, the dorsal blood vessel lies below them (Fig. 33, No. 2-6; Fig. 34, No. 7-12; Fig. 41, No. 103, 108). Its diameter in the midgut region is about 40 µ. This vessel has only remnants of mesenteric suspension membranes. In the region of these dissepiments it can be seen in all clitellar somites and in those of the midgut and hindgut regions (except in the 2 most posterior body dissepiments) that a short membrane of varying width is connecting the blood vessel wall with the intestinal wall (Fig. 34, No. 7). These membranes consist of mesenchyme in which 1 terminal branch of the dorsal dissepiment muscle cells (dsz) is embedded on each side. Thus the structure is very similar to that described for the ventral blood vessel, except that the latter have dorsal, the former ventral mesentery sectors. In the entire 3rd preclitellar somite (8) and in the posterior part of the 2nd preclitellar somite (7), the ventral mesentery sector is generally fully developed, i.e. as a relatively thin mesenchymatous lamella that is, of course, covered on the outside by coelothelium (Fig. 33, No. 5). Further cephalad, where the movable foregut begins, this lamella disappears and is replaced by the dorsal fold of the same mesentery (Fig. 33, No. 4). The latter appears as a thin mesenchymous membrane connecting the inner body mesenchyme with the dorsal blood vessel. It extends through the anterior sector of the 2nd preclitellar somite (7) and through the 1st preclitellar somite (6) as well as through the 5th (Fig. 33, No. 3) and 4th somite of the head region. In the head somites remnants of the ventral mesentery sector can be recognized, so that in some parts a full dorsal mesentery is present.

Especially favourable for observing the structure of the dorsal blood vessel is the section situated in the 5 anterior somites of the hindgut region (Fig. 41, No. 108). Here it is resting closely against the hindgut wall. Several times in each somite it forms an open connection with the intestinal blood sinus (Fig. 34, No. 12) that has been described above. The first such connection is in the dissepiment (dsp_{19}) between the 8th somite (19) of the midgut region and the 1st somite (20) of the hindgut region.

The connection itself is accomplished (Fig. 39, No. 71) by perforating the wall of the ventral blood vessel (dg) medially or slightly laterally, and by perforating the corresponding part of the wall of the intestinal blood sinus (ds), causing the lumen of the blood vessel to merge here directly with the lumen of the intestinal sinus. The peritoneal coating (ct) of the intestinal tract continues without interruption on the dorsal blood vessel, and the outer lamella of the mesenchyme layer of the hindgut merges through the described opening with the blood vessel where it forms the vessel's only own wall layer, since neither a muscle layer nor an intima are present in the wall here. The peritoneal epithelium (ct) of the vessel wall quite resembles that of the parietal coelothelium. The mesenchyme layer (ms) consists of a thin lamella of a transparent, gelatinous substance.

In the blood vessel lumen the same cell elements (bz) are often found resting against the vessel's marginal lamella; they also occur freely suspended in the blood, and their structure is quite identical with the already described coelomocytes (cz). These are the only free cells in the blood vessels (Fig. 39, No. 71).

The dorsal blood vessel of the Glossosiphonida has quite the same structure as in *Acanthobdella*.

At the dissipiment (dsp_{24}) between the 5th (24) and 6th (25) somite of the hindgut region, the dorsal blood vessel divides into 2 branches (Fig. 41, No. 104, 108), which in the 6th somite extend gradually ventrad; they have the same structural characteristics and relationships to the intestinal blood sinus as described above for the dorsal blood vessel itself.

Cephalad from the 8th somite (19) of the midgut region to the 2nd preclitellar somite (7), the dorsal blood vessel runs as an entirely enclosed tube, showing exactly the same structure as in the hindgut region (Fig. 39, No. 76). Only in the dissepiment between the 2nd (10) and 3rd (11) clitellar somite, a relatively large circular muscle cell occurs in the surrounding mesenchyme, forming a type of sphincter at the dorsal blood vessel (Fig. 34, No. 9).

On the other hand, at the boundary between the 2nd and 3rd (8) preclitellar somite we find very significant changes in this respect (Fig. 39, No. 77). It can be seen that from this point on, the blood vessel lumen contains a special inner layer (is) which is resting against the marginal lamella of the mesenchyme, forming a very thin membrane. On the outside this membrane are found the cells which generated it (is*) in the form of protoplasmic proliferations about 15 µ in height and 30-40 µ in width, whose finely grained, easily stained protoplasm contains the oval nucleus which measures about 10 µ in diameter and has many chromatin granules. These cells are never present in the said sectors of the dorsal blood vessel. The layer in question is homologous to the inner layer of the ventral blood vessel or the transverse blood vessels.

In the mesenchyme layer (ms) circular muscle fibres (rm) also occur at the margin between the 2nd and 3rd preclitellar somite. Their nucleate sector is about 20-30 µ in width and up to 40 µ in height; it projects from the fibre plane toward the inner layer. Transversely the cell body gives off 2-3 processes in the opposite direction which span the blood vessel. In their inner surface which faces the vessel lumen is the fibrillar-contractile layer which is seen as very thin lamellae and which also continues to the nucleate protoplasm proliferation, the latter usually being without lamellae over a distance of varying length. Outside the contractile-fibrillar layer is entirely absent from the cell and its processes. The protoplasm of these muscle cells is finely grained and stains very well; in the processes it is transversely striated. The nucleus is oval in shape, has a diameter of about 20 µ and a length of about 25-30 µ; it contains numerous chromatin granules of varying dimensions.

A comparison between these structural characteristics of the dorsal blood vessel of *Acanthobdella* and those of the corresponding sector of the dorsal blood vessel in Glossosiphonida shows that they are almost completely identical. The author again refers to the literature summary provided by A. LANG (1903, pp. 253-259) and agrees with his views regarding the musculature of the dorsal vessel, although his opinion varies considerably as far as the inner layer of the blood vessel wall is concerned.

The wall of the dorsal vessel of the 2nd preclitellar somite (7) keeps the described structure as far as the supraesophageal ganglion mass, i.e. to the middle of the 3rd head somite. Here the circular muscle layer gradually decreases, and near the supraesophageal ganglion mass the vessel consists only of the inner (is) and outer (ms) mesenchyme layer, thus having the same structure as the ventral blood vessel in its most anterior sector. In this state the dorsal blood vessel continues cephalad, passing between the supraesophageal ganglion mass and the esophagus.

Shortly before the pharynx it divides into its 2 branches (qg_1) resting closely against the foregut; the branches extend downward in the shape of an arc, merging with the corresponding branches of the ventral blood vessel where they form the 1st pair of transverse blood vessels (Fig. 38, No. 63; Fig. 41, No. 103).

In addition to these pharyngeal rings, the dorsal blood vessel (dg) also gives off 4 pairs of transverse blood vessels (qg$_{2-5}$; Fig. 41, No. 103), all of which are provided over a short distance with circular muscle fibres at the point where they leave the dorsal blood vessel. These fibres are formed by about 2 muscle cells which resemble those of the dorsal blood vessel. However, later these transverse vessels show the regular above described structure of their ventral sectors. A. OKA (1894) found a similar situation in the Glossosiphonida.

The 2nd pair of transverse vessels (qg$_2$) separates from the dorsal blood vessel at the margin between the 2nd and 3rd head somite (Fig. 41, No. 103). To reach its ventral sector, each transverse vessel first runs cephalad in the dorsal coelom sector inward of the first 2 pairs of protractors (pr$_{1,2}$), then in the body mesenchyme toward the posteriorly displaced ends of the dorsoventral muscle cells (dvm$_2$) of the 2nd somite, and finally, curving around the latter, in the coelom behind the central pair of chaetae (bsz$_2$) of the 2nd somite (Fig. 33, No. 2) and behind the pharyngeal connective ventrad. The 3rd pair of the vessels (Fig. 38, Fig. 67 qg), which leaves the dorsal blood vessel in the most anterior sector of the 4th head somite, extends over its entire length in the coelom near the esophagus, inwardly of the 3rd protractor pair (pr$_3$) and the dorsal secretory ducts of the latter, each vessel forming a sort of arc pointing forward (Fig. 41, No. 103 qg$_3$). The 4th pair of transverse vessels (qg$_4$) also lies in the coelom freely. They separate from the dorsal blood vessel in the anterior sector of the 5th head somite, run cephalad and outside the dorsal secretory duct clusters of the esophagus; then they curve around the inner dorsoventral muscle cells (dcm$_1$) of this somite and finally ventrad where they meet their parts coming from the ventral blood vessel. The simplest route is taken by the transverse vessels of the 5th pair (qg$_5$). From the dorsal blood vessel they extend into the anterior sector of the 1st preclitellar somite (6), they form inconspicuous arcs in the posterior sector of the 5th head somite and thus merge with their ventral parts.

Thus the head end of *Acanthobdella* contains 4 pairs of transverse blood vessels arranged quite metamerically according to their places of origin in the longitudinal blood vessels, namely between the 2nd and 3rd, 3rd and 4th, 3rd and 4th, 4th and 5th head somites and between the latter and the 1st preclitellar somite. The last pair of vessels is a particularly good example for explaining their position more closely: it is perfectly clear that it belongs to the dissepiment between the 5th head somite and the 1st preclitellar somite because it leaves the septum region only in its loop-like path. Such relationships to the corresponding dissepiments can be more or less clearly distinguished in the other transverse blood vessels as well. Thus the head end of *Acanthobdella* has 4 pairs of transverse dissepiment vessels whose path is subject only to relatively insignificant secondary changes.

As demonstrated already, the 1st pair of transverse blood vessels is more intimately related to the esophagus, in which it differs from the other 4 pairs just described. However, this difference is not sufficient to question their homology to the other pairs of vessels. These are only changes which look like adaptations of the transverse dissepiment vessels to the special structural characteristics of the anterior end. The author therefore regards this anterior pair of transverse blood vessels as a pair of vessels of the dissepiment between the 1st and 2nd head somite.

The characteristic found in the Glossosiphonida can be derived without difficulties from this metameric arrangement of the 5 pairs of transverse blood vessels in *Acanthobdella*. First of all, the proboscis vessel ring of the Glossosiphonida in its relationship to the foregut is almost completely identical to the 1st transverse blood vessel pair of *Acanthobdella*. The difference is due only to the formation of the proboscis fold in the Glossosiphonida which forces the proboscis vessel of the latter to describe a loop of varying length before entering the proboscis wall. This causes an even greater elongation of the vessel, since inside the proboscis it continues forward to its anterior end where the vessel ring of the 1st pair of transverse vessels is finally formed. Another result of this characteristic seems to be that the proboscis vessel of the Glossosiphonida divides from the dorsal blood vessel dorsally in the manner of a relatively insignificant lower branch, to enable it to be closer to its entry point into the proboscis. But ventrally the original topographic relationships have remained the same, and these are a direct continuation of the ventral blood vessel.

The peculiarities of the proboscis vessel of the Glossosiphonida confirm the above explanation that the characteristics of the Rhynchobdellid proboscis have probably evolved from a condition similar to that in *Acanthobdella* through the extraordinary development of the buccal cavity and foregut fold which in *Acanthobdella* are inconspicuous.

The following 4 pairs of transverse blood vessels of the Glossosiphonida differ from those in *Acanthobdella* only in the exceptional loop-like creases and their departure points from the dorsal or ventral longitudinal blood vessel. Regarding this loop formation, the following comments by A. OKA (1894, p. 113) should be quoted here: "In very young individuals, they" [the most posterior pair of transverse vessels] "reach only as far as the 16th segment, while in adults they go as far as the 22nd or 23rd segment", which certainly indicates the secondary nature of these changes. The displacement of the departure points of the transverse vessels seems to be due to the posterior shift of the departure point of the dorsal proboscis vessel part of the dorsal blood vessel. In the ventral blood vessel, the departure points of all transverse vessels have come close together, although in total they have been shifted caudad, probably caused by the development of the attachment disk. For a better understanding of this apparently complicated situation, reference is made to the relevant illustration in OKA's paper (1894, Fig. 24, Plate 5).

According to this, the anterior sector of the blood-vascular system in *Acanthobdella* and in the Glossosiphonida would be formed according to the same type, since the following are present: the dorsal and ventral longitudinal blood vessels and 5 pairs of transverse blood vessels connecting the same. *Acanthobdella* has by far the more primitive characteristics in that these vessels have a strictly metameric arrangement, corresponding to the 5 most anterior dissepiments. This indicates an almost direct link with the Oligochaeta.

Also of the same type in *Acanthobdella* and in the Glossosiphonida are the dorsal and ventral blood vessels and the intestinal blood sinus which were described above together with the intestinal tract. The relationships between the dorsal blood vessel and the intestinal blood sinus, too, are the same in both cases. However, the 5 vessels connecting this sinus and the ventral blood vessel have disappeared completely in the Glossosiphonida. In *Acanthobdella* these vessels are slightly reduced, again resembling the more primitive characteristics found in the Oligochaeta.

We will now discuss the blood vessels of the posterior body region (Fig. 41, No. 104).

The two posterior branches of the dorsal blood vessel deviate slightly from the dorsal median line and enter the body mesenchyme at the last body dissepiment (Fig. 34, No. 13; Fif. 41, No. 108). To this point they keep the characteristics of the dorsal blood vessel shown during its path through the intestinal region. However, in the mesenchyme their structure immediately changes: here they have the structure of the ordinary above described transverse blood vessels or of the most anterior parts of the dorsal and ventral blood vessels.

In the mesenchyme these branches span the hindgut near its merger with the endgut; then they unite once again (Fig. 41, No. 101). The ring vessel thus formed gives off transverse blood vessels. At first one vessel (qg_1) branches off on each side, extending ventrad in the inner mesenchyme above the longitudinal muscles until in the attachment disk region it enters the mesenchymatous interspace between the medial and paramedial muscle bundles. Here the pair of vessels unites with the said most anterior pair of the transverse blood vessels coming from the ventral blood vessel (Fig. 34, No. 14). These extend through the coelom and the mesenchyme directly into the corresponding muscle interspace. The ventral sectors of the 2nd and 3rd pair, whose route coming from the ventral vessel was described in detail above, also extend from the transverse vessel into the mesenchymatous interspaces, the 1st (qg_2) mediad from the ventral intermediate line, the 2nd (qg_3) ventrad from the lateral line (Fig. 41, No. 104). The dorsal sectors of these transverse vessels are united over a short distance and thus have a common root, originating in the corresponding dorsal branch. In the body mesenchyme of the attachment disk region these two transverse vessels separate near the lateral longitudinal muscle strand, one entering the interspace at the lateral line, the other deviating ventrad to enter the interspace at the intermediate line. Here they merge into the corresponding ventral sectors of the vessel, forming the 2nd and 3rd pair of transverse vessels of the attachment disk region (Fig. 34, No. 14). The 4th and last pair (qg_4) is given off by the dorsal branches just before their point of union behind the intestine. Usually an anastomosis exists between the right and left vessel of this last pair near the dorsal end: while the right vessel enters the mesenchymatous interspace of the attachment disk region laterad of the dorsal intermediate line, the left vessel enters the corresponding interspace of the other side only after giving off a separate vessel which extends further caudad at the dorsal median line. Having arrived in the interspace at the intermediate line, the vessels of the 4th pair meet the ascending ventral sectors of the same pair and unite with these. However, the branch (dg) extending along the dorsal median line units in the attachment disk region with the terminal sector of the ventral blood vessel (vg), thus forming a kind of medial unpaired vascular loop between the ventral and dorsal longitudinal blood vessels. Therefore the latter could be regarded as the terminal sector of the dorsal blood vessel which, after reunification of the branches surrounding the intestine, extends caudad and gives off the left transverse vessel of the 4th pair.

Each of the described 9 vessel arcs gives off one longitudinal branch vessel extending caudad which continues in the mesenchyme to the edge of the attachment disk (Fig. 35, No. 15; Fig. 41, No. 104). Here these 9 branch vessels are connected with each other by a ring vessel (vg) embedded in the mesenchyme between the separating longitudinal muscle fibres (Fig. 35, No. 16).

Thus the attachment disk region of *Acanthobdella* contains 4 pairs of transverse vessels and 1 unpaired median vessel arch. As mentioned, the latter in all probability represents the terminal union of the dorsal and ventral blood vessels, i.e. a non-metameric formation of the posterior body end, while the transverse blood vessels are certainly metameric formations, as indicated by their strictly segmental departure points from the ventral blood vessel. On the dorsal side these original relationships are more or less obscured. The same applies in the attachment disk region due to the radial arrangement of the vascular loops and the presence of the ring vessel, which certainly has to do with the general radial design of the attachment disk and can be regarded as a secondary adaptation to the function of the latter.

According to A. OKA (1894), the situation is very analogous in the attachment disk area of certain Glossosiphonida, for example in *Protoclepsis tessellata* and *Hemiclepsis marginata*, where 7 pairs of vascular loops are present in the same arrangement as in *Acanthobdella*. In that case they must all be metameric transverse vessels, judging by the development of the attachment disk. This indicates that in *Acanthobdella*, in keeping with the 4 pairs of transversal vessels, the attachment disk region must have developed from the union of 4 metameres or somites, which is also confirmed by the results of our examination of the nervous system.

Although by and large, the structural characteristics in the vascular system of the attachment disk region are the same in *Acanthobdella* as in the Glossosiphonida, the specific differences found in this region are far greater than in the other sectors of the vascular system. One reason is that the attachment disk region of *Acanthobdella* consists of only 4 somites, while it consists of 7 somites in the Glossosiphonida and all other Hirudinea. However, it should be noted here that A. OKA (1894) reported finding only 4 pairs of transverse vessels in *Glossosiphonia complanata*, *Gl. bioculata*, and *Gl. heteroclita*, and only 3 pairs of such vessels in *Gl. papillosa*. The most important difference in comparison with all other Hirudinea is the presence of medial vascular loops and of a ring vessel in *Acanthobdella*. The absence of such a ring vessel in the Glossosiphonida has to be attributed to the formation of a corresponding coelom sector in which the subepithelial coelom sinuses seem to have assumed certain functions of the blood-vascular system.

In summary in can be concluded that the blood-vascular system of *Acanthobdella* clearly represents the general Hirudinean type, while certain more primitive characteristics present in this species indicate a close affinity to the Oligochaeta.

12. The nephridial system

A KOWALEVSKY (1896, p. 267) wrote as follows about the nephridia of *Acanthobdella*: "Dans les dissépiments sont placées les nephrides qui s'ouvrent à l'extérieur par des ouvertures placées sur les côtes du corps, aux limites des somites. Les nephrides ne possédent pas de vessies urinaires, et je n'ai pas trouvé des entonnoirs vibratils à leur bout intérieur". That is all he wrote on this subject.

According to the author's own observations, the nephridia (nph_{6-19}) are distributed in the body of *Acanthobdella* as follows (Fig. 33, No. 1): The 1st (6) and 2nd (7) preclitellar somites each have 1 pair of well-developed nephridia, while in the 3rd preclitellar (8) and in the 2nd (10) and 3rd (11) preclitellar somites only their excretory ducts appear as small invaginations in the skin epithelium. The actual excretory sector in the narrower sense is completely lacking in the latter. However, the 3rd clitellar somite sometimes contains a pair of nephridia reduced to an absolute minimum (Fig. 39, No. 82) in which their excretory sector is represented only by a single nephridial cell (npz) on the short, tubular invagination of the skin epithelium and thus in the inner body mesenchyme between the longitudinal muscles. The 1st clitellar somite (9) contains no traces of nephridia. All 8 somites of the midgut region contain 1 pair of well-developed nephridia each. They never occur in the head somites or the somites of the hindgut and attachment disk region.

Taking into account the number and position of nephridia in the other Hirudinea, it can be seen that as in *Acanthobdella*, the 1st pair of nephridia is in the somite (6) which is innervated by the 2nd ordinary ganglion of the ventral cord. This point is confirmed by almost all the findings of other authors. The present author was able to observe the same characteristic in *Protoclepsis*, in *Hemiclepsis marginata*, and in *Hirudo medicinalis*. The Ichthyobdellida form an exception: according to A. BOURNE (1884) and S. APATHY (1888) their nephridia are found to begin only in the 1st somite of the midgut region. The present author can add that he has observed the 1st pair of nephridia in the 1st mid body somite of *Pisciola geometra* and *Cystobranchus* sp.

This complete disappearance of the nephridia in the preclitellar somites of Ichtyobdellida is only a further step in the process characterized by the absence of nephridia in the clitellar somites.

The reduction of nephridia is carried to the extreme in the Ichthyobdellida where they are completely lacking in the clitellar region. According to A. OKA (1894), *Glossosiphonia complanata* and *Gl. heteroclita* have nephridia only in the 3rd clitellar somite, while they are lacking in the

1st and 2nd somites. The same author reports that in *Protoclepsis tessellata, Hemiclepsis marginata* and *Glossosiphonia stagnalis*, nephridia are present in all clitellar somites. W. CASTLE (1900) claimed that they had been lost in the 3rd clitellar somite of *Gl. stagnalis.* According to the present author's observations, the nephridial apertures have been eliminated in all 3 clitellar somites in *Protoclepsis*, and in *Hemiclepsis marginata.* It should also be mentioned that in Glossosiphonia (Clepsina), APATHY (1888) observed nephridia in the 1st clitellar somite only. Without discussing these findings in detail, we can see that the nephridia are more or less reduced in the clitellar somites of the Glossosiphonida.

In the Gnathobdellida on the other hand, nephridia occur in all somites of the clitellar region. Only APATHY (1888, p. 195) remarked in this respect: "Among the Gnathobdellida, *Nephelis* (*Herpobdella*) possesses no external nephridial apertures in any clitellar somite". However, his statement does not seem to be accurate, since the other authors unanimously agree that in this genus the somites of the clitellar region do have nephridial openings (R. BLANCHARD, 1894; A. GRAF, 1894 for *Herpobdella atomaria* and *H. octoculata*, C. BRISTOL, 1898 for *H. lateralis*). The present author himself has observed the nephridia and their apertures in all 3 clitellar somites in one individual of *Herpobdella atomaria* and in one *Herbobdella* species from Lake Baikal.

Thus the Hirudinea can be divided into 2 groups as far as the distribution of nephridia is concerned. In one group, namely the Rhynchobdellida, the nephridia have more or less disappeared from the clitellar somites. In that group, the culmination is reached in the Ichthyobdellida whose nephridia are absent in all somites of the clitellar region. Another group is formed by the Gnathobdellida in whom the

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINEE A LA PUBLICATION

nephridia are quite regularly developed in all somites. Thus *Acanthobdella* is closely related to the former, namely to the Glossosiphonida from whom they differ only in the disapperance of the nephridia in the 3rd preclitellar somite.

Although *Acanthobdella* resembles the Hirudinea in the distribution of the anterior nephridia, this form differs in that in the latter the last pair of nephridia lies in the most posterior somite (19) of the midgut region, while in the former the last nephridia are always in the somites of the hindgut region. However, these characteristics do not prevent us from easily recognizing in *Acanthobdella* the general Hirudinean type as far as number and position of the nephridia is concerned.

The typically formed nephridium of the mid body of *Acanthobdella* has 2 sharply differentiated sectors (Fig. 40, No. 95): the very short sector devoted only to elimination, and the very considerable actually excretory sector.

The former represents an invagination of the skin epithelium (ep) which enters on the ventral intermediate line to the inner body mesenchyme through the circular (rm), diagonal (dm) and longitudinal (lm) muscle layers (Fig. 39, No. 82). A sort of widening of its proximal part, found in many Hirudinea, never occurs in *Acanthobdella*, and in this respect, the latter resembles the Glossosiphonida. The cells of the said nephridial sector are ordinary skin epithelium cells of cylindrical or cubic shape.

The excretory sector of the nephridium forms a repeatedly coiled strand whose cells are arranged uniserially in succession, perforated over almost the entire distance of this sector, except in the most proximal part, by a single intracellular canal. Regardless of the various forms of differentiation, all cells (npz) have general structural characteristics , which make it easy to distinguish the unique tissue of the excretory cells of the nephridia from all other elements of the body (Fig. 39, No. 78-81).

The said sector begins proximally in the mesenchyme of the dissepiment, slightly dorsad and laterad of the ventral coelom sinus (Fig. 40, No. 96), whence it ascends in the dissepiment as a coiled strand up to the lateral line of the intestine. Over its entire length, this piece is formed by very large cells (npz_1; Fig. 39, No. 78a, b); the margins between these are very poorly differentiated if visible at all. The protoplasm of these cells is very finely grained and stains very well. When the object is stained with osmic acid, the plasm is found to contain sparsely distributed droplets of a substance that turns a deep black when stained and assumes a fat-like appearance. At the periphery of the cell, except for the parts bordering on the next anterior or posterior cell, the protoplasm layer is sharply differentiated and striated, the stripes running vertically to the cell surface. In some cases the striation is so characteristic that it resembles true tubules leading into the cell body from outside. Nevertheless the cell has a very sharp contour from the outside, due to the very fine marginal lamella of the accumbent mesenchyme. The oval or roundish nucleus which here reaches up to 40 µ in diameter, is richly provided with chromatin granules, between which 2, 3 or more nucleoli (plasmosomes) are present.

A peculiarity of this proximal nephridial section, which distinguishes it from the rest, is the presence of a system of ramified, anastomotic tubules in the cell. Beginning as very minute cavities near the periphery of the cell, they enlarge gradually, unite with each other and finally end in various places in the central canal that extends through the entire length of the respective nephridial section and continues directly through to the next section. The anastomoses between the tubules look very irregular, forming a network which may extend throughout the entire nephridial sector. All these tubules, including the very smallest, are of identical structure, and their walls are not differentiated in the accumbent protoplasm, where they form nothing but hollows. The oval or roundish cross section of the central canal reaches a diameter of up to about 6 μ (Fig. 38, No. 78a, b; Fig. 40, No. 95 npz_1).

The boundaries between the individual cells could not be recognized with the methods used by the author, and only the presence of the regularly arranged nuclei indicates where the corresponding cells are situated. In the centre is the cell cord, perforated lengthwise by a single canal. The protoplasmic walls of the canal are not differentiated; the canal is usually of roundish shape, about up to 6 μ in diameter, so that its protoplasmic walls are up to 4 μ thick. As in the nephridial cells of the initial sector, their protoplasm is finely granulated, stains well, contains droplets of the same fat-like substance, and is very finely striated at the periphery. In some places the protoplasmic walls have thickened sections in which the oval or roundish nucleus is situated whose diameter reaches up to 20 μ in diameter. Its structure is as described above. Thus the excretory cells of the nephridia are characteristic of their type, albeit much smaller due to the insignificant thickness of the protoplasmic cell parts.

Half-way along the intestine the said nephridial sector (dmt) ascends in the dissepiment up to the dorsal coelom sinus (Fig. 40, No. 95, 96). Here it turns, always running close to the coelom wall, caudad to the inner body mesenchyme, forming an inconspicuous arc, thus leaving the dissepiment. Then this section turns downward, without changing its structure, parallel to the former path, to the lateral line of the intestine. From this point the nephridial cord (npz_1*) extends ventrad in the former direction almost to the ventral longitudinal musculature, where it describes a sharp curve, repeats the same path (npz_1*), and returns to the departure point of the respective nephridial sector, i.e. to the lateral line of the intestine in the dissepiment. The two loops thus formed are closely accumbent to each other. Since their structure is quite similar seen dorsally from the lateral line of the intestine, these nephridial sectors could easily be mistaken for a single cord penetrated by 2 canals (Fig. 39, No. 79). However, with good fixation and staining, the margins of the two loops are clearly differentiated; the loops also more or less deviate from each other in several places. The parts of these loops lying ventrad from the lateral line of the intestine (npz_1*, npz_2*) differ in structure from that of the above described: their cells are larger (Fig. 39, No. 80; Fig. 40, No. 95), so that their roundish cross section has a diameter of about up to 30 µ; their central canal reaches a diameter of up to 20 µ, and the protoplasmic walls reach a thickness of about 6 µ. Here, too, their oval or roundish nucleus is larger and reaches about 25 µ in diameter. In connection with the larger size, the said structural characteristics typical for the nephridial cell are also more pronounced in the protoplasm. The two transitional points between the ventral (npz_1*, npz_2*) and the dorsal parts are well defined (Fig. 40, No. 95) because usually the narrow central canal abruptly merges into the wide canal, and vice versa.

We will now follow the further path of the said nephridial sector. From the lateral line of the intestine it extends (npz_2) ventrad in the dissepiment, close to the nephridial sector with the ramified tubules to the beginning of the latter (Fig. 40, No. 95). At this point the cells (npz_2) of the same are very large and well-developed (Fig. 39, No. 78c). Their central canal has a diameter of about up to 20 µ, and the walls are about 10 µ thick. The oval or roundish nuclei reach a diameter of up to 40 µ. This nephridial sector turns caudad and ventrad, quickly narrowing, leaving the dissepiment and extending in the body mesenchyme up to the ventral parts of the said nephridial loops. Here the cells (npz_2) reach a diameter of about 15 μ, so that the central canal is again about 6 μ wide, and the protoplasmic walls have a thickness of 4 μ (Fig. 39, No. 78a, b).

Once they have arrived at the loops, the cells become larger again, and the central canal also widens; resting closely against the 2 cell cords of the loops, the nephridial sector ($npz*_3$) ascends with them to the lateral line of the intestine, so that the 3 cell cords together form the posterior leg of the nephridium (Fig. 40, No. 95, 96). Here the structural characteristics become very similar to those of the 2 adjacent cords described above, with the possible exception that the cells (npz_3*) sometimes appear somewhat larger and the central canal somewhat wider (Fig. 39, No. 80).

Half way along the intestine this cord (npz_3*) separates from the two adjacent cords of the posterior leg and returns to the dissepiment (Fig. 40, No. 95), i.e. cephalad, and at the upper end of the nephridial sector with the ramified tubules it is (npz_3) resting closely against the latter and the said widened part of its sector, forming the anterior leg of the nephridium together with both of these (Fig. 40, No. 95, 96). The dorsal transitional part is very similar to the ventral, i.e. it has a significant narrowing of the canal and a similar reduction in the size of the cells. Subsequently this part extends downward to the level of the ventral coelom sinus where it merges with the last part leading to the skin epithelium depression. Along its path it forms insignificant creases, as does the adjacent nephridial sectors. Its structure differs from that of the described parts only in that its cells (npz_3) are very large and more richly provided with fat-like droplets (Fig. 39, No. 78a, b). The canal has an oval or roundish cross section and a diameter of about up to 40 µ, while the wall is about 15 µ thick. The peripheral, radially striated layer is as well-developed in the wall as in the adjacent nephridial sector, and the oval or roundish nucleus reaches a diameter of up to 35 µ.

The part of this nephridial sector extending to the skin epithelium invagination extends in the inner body mesenchyme caudad from the dissepiment level to the margin between the 1st and 2nd annulus of the respective somite (Fig. 33, No. 1; Fig. 40, No. 95, 96). Its cells are of medium size (Fig. 39, No. 81). The lumen of the canal is about 20 µ in diameter, its wall about 8 µ thick. Here, too, the nephridial cells are characteristic of the type found in all other nephridial sectors. Here, the oval or roundish nuclei reach up to 25 µ in diameter. The intracellular canal of the last cell of this sector opens between the epithelial cells into the tube of the skin epithelium invagination.

It is known that In the Hirudinea the nephridia are formed according to a well-developed, general type with some deviations only in the Hirudinida and Ichthyobdellida. Disregarding those, we will now compare the author's results regarding *Acanthobdella* with the results obtained by various other authors regarding the nephridia of the other Hirudinea.

A surprising similarity is found when the nephridium of *Acanthobdella* is compared with that of *Glossosiphonia* as shown in the studies by A. BOURNE (1884) or A. OKA (1894). The only difference is the presence in the latter of the funnel apparatus and of a nephridial sector with ramified tubules (the so-called BOURNE's testicular lobe) which extends between the funnel and the anterior leg of the nephridium. As noted above, KOWALEVSKY (1896) also correctly identified the absence of the funnel apparatus as a peculiarity of the nephridium of *Acanthobdella*

This fact, however, does not constitute a fundamental difference in terms of the general Hirudinean type of the nephridium, since the connection between the funnel apparatus and the actual excretory sector, at least in the morphological sense, is poorly developed here at any rate.

Only R. LEUCKART (1894) and his students OKA (1894) and D. McKIM (1895) claim that they were able to observe a direct transition of the nephridial tubules into the capsule cavities. However, only 1 illustration by OKA (Fig. 57) and 2 illustrations by McKIM (Fig. 20 and 33) were instructive, while the others were insufficient. These authors emphasize how difficult it is to prove this. Almost at the same time, BOURNE (1893, p. 559) wrote that the funnel apparatus forms a part of the nephridum, but that "the communication between its lumen and that of the nephridial tubules is, generally at any rate, obliterated". In contrast to these authors, H. BOLSIUS (1891, 1896*) denied any anatomical or physiological connection between the funnel apparatus of Hirudinea and the excretory nephridial sector.

A GRAF (1899, p. 256 and 257), who found it "of special significance to clarify the connection between the funnel and the other parts of the nephridium", wrote that "the objection raised by BOLSIUS against a connection of the funnel with the glandular cells of the nephridium was completely justified, since it is quite correct that the receptaculum is always surrounded by a closed wall and only has an opening where the stem cell opens into the funnel crown". Using different wording, GRAF, after perusing the available literature and following his own observations, concluded that the funnel apparatus of the Hirudinea is anatomically independent of the excretory nephridial sector. Following this, A KOWALEWSKY (1900, p. 38) stated that "d'après leur structure et leur fonction les cellules de la capsule n'ont absolument rien de commun avec les

cellules des néphridies". E. BRUMPT (1900, p. 406) also wrote: "Chez les Gloososiphonides j'ai toujours trouvé ces organes en contiguité, mais je n'ai jamais vu la continuité de ces diverses parties comme l'ont soutenu les nombreux adversaires de BOLSIUS ... Chez les Herpobdellides et *Pontobdella* la continuité n'existe pas davantage". Finally, L. CUÉNOT (1902, p. 92) wrote: "Les organes cilio-phagocytaires (capsules néphridiennes) des Hirudinées sont aussi au voisinage des néphridies, mais sans communication avec elles".

The present author has investigated the nephridial system in *Hemiclepsis marginata*, *Glossosiphonia complanata* and, in much detail, in *Protoclepsis tessellata*. In all these species the funnel apparatus is not directly resting against the excretory nephridial sector, so that there can be no question here of an open communication between these formations: they are separated from each other by a thin mesenchyme layer. However, when the funnel apparatus directly borders on the excretory nephridial sector, the nephridial tubules also seem to be entirely independent of the cavities of the funnel apparatus, and they are separated from each other on one side by the capsule wall, on the other side by the intact seam of the nephridial cell.

Thus the conclusions reached by LEUCKART, OKA and McKIM have proven to be in error, and there is justification for the views held by all subsequent authors that the funnel apparatus of the Hirudinea is anatomically independent of the excretory sector of the nephridium.

This independence is further substantiated by the absence of the funnel apparatus in some nephridia, especially in the 1st nephridium of the Glossosiphonida, as observed by OKA (1894) in *Glossosiphonia complanata* and *Gl. heteroclita*, by KOWALEVSKY (1900) in *Haementeria costata*, by BOLSIUS (1900) in *H. officinalis*, and by the present author in *Protoclepsis* *tessellata* and *Pr. maculosa*. As far as *Hirudo* is concerned, LEUCKART (1894), O. BÜRGER and McKIM (1895) reported the complete disappearance of the funnel apparatus in all nephridia of the clitellar region. According to GRAF (1894), *Herpobdella* shows the same characteristics, which the present author could confirm in *Herp. atomaria*. All findings by these authors agreed that all traces of the funnel apparatus have disappeared in most Ichthyobdellida[1].

Thus the absence of the funnel apparatus in *Acanthobdella* is not only quite in keeping with the structural characteristics occurring in Hirudinea, but this fact is actually an indication that the general Hirudinean type of nephridia has been developed in *Acanthobdella*, because this expresses to a certain degree the anatomical independence of the funnel apparatus and the excretion tube.

In addition to schematic representations of the nephridium of the Glossosiphonida supplied by BOURNE (1881) and OKA (1894), this organ has been illustrated in the studies by O. SCHULTZE (1883), F. VEJDOWSKY (1883) and GRAF (1899). SCHULTZE's illustrations were quite in keeping with those by BOURNE and OKA.

VEJDOWSKY illustrated the nephridia of *Protoclepsis tessellata*, *Hemiclepsis marginata* and *Glossosiphonia stagnalis* (*bioculata*). Of these three species, the present author has examined *Pr. tessellata* in detail, as mentioned, and he can now confirm that its typically formed nephridium of the mid body is quite in accordance with the general type of this organ as illustrated by BOURNE and OKA. An insignificant difference is the position of the anterior and posterior nephridial legs which are at an almost right angle to each other, and not parallel. However, the illustration by VEJDOVSKY deviates so much from those of BOURNE, OKA and the present author that no similarity can be found between them. The explanation for this may be that VEJDOWSKY illustrated the nephridium of the last pair ("14th pair of young individuals") which may not be typically formed. In regard to *H. marginata* and *Gl. stagnalis*, the present author cannot make any definitive statements, but he believes that OKA's findings are probably more accurate, since they agree with those of SCHULTZE and BOURNE.

---

[1] The author feels that the embryological studies by BÜRGER (1891, 1894, 1902), which clearly indicated morphological union of the funnel apparatus with the excretory nephridial sector, require detailed further study.

In the illustration of the nephridium of *Glossosiphonia hollensis* by GRAF, the nephridium is seen in a top view, which makes them appear significantly different from the illustrations of BOURNE and OKA which presented them in the transverse plane of the body. Otherwise, the arrangement of nephridial parts is very similar to that just described in regard to *Pr. tessallata*. Taking everything into account, the general nephridial type of the Glossosiphonida is also easily recognized in GRAF's illustration, although it does not seem to depict the individual canal parts with complete accuracy. Thus the schematic representations by BOURNE and OKA present the facts more accurately.

In terms of all other structural characteristics of the nephridia of the Hirudinea, the authors quite agree. The nephridium of the Hirudinea consists of a cord of uniserially arranged cells which have a particularly well defined structure, and the case is quite similar in *Acanthobdella*. The cord is perforated by a single central canal in addition to which the anterior nephridial sector contains smaller tubules. These relationships were seen differently only by H. BOLSIUS (1890, 1892) who thought that the nephridial cells contain 1, 2 or 3 canals which are by no means creases of one and the same cell cord of the nephridium. However, this opinion by BOLSIUS is rejected as erroneous by all other authors, and the present author, too can cite his findings in *Pr. tessellata* as proof against BOLSIUS. In this respect, the structural situation in *Acanthobdella* is quite in keeping with the general Hirudinean type. An insignificant deviation could be the presence of anastomoses between the tubules in the anterial nephridial sector of *Acanthobdella*, which create a sort of network, while in most Hirudinea these tubules ramify without forming anastomoses. Only VEJDOWSKY found a similar situation in *Gl. stagnalis*, and GRAF (1899, p. 301) described similar relationships in other Glossosiphonida. This difference, too, is therefore losing its significance.

Cilia are entirely absent in the nephridial canals of the Hirudinea, a major difference in terms of the Oligochaeta and other annelids in which the presence of cilia seems to be characteristic as far as the nephridial canals are concerned. *Acanthobdella* is also lacking cilia in the nephridial canals, an important and clear indication that the nephridia of this species are of Hirudinean type. Another characteristic in which the nephridia of the Oligochaeta differ from those of the Hirudinea is the presence of a funnel apparatus which is always in open communication with the nephridial canal. The absence of a funnel, known for example in *Chaetogaster*, is a rare exception.

However, by and large it should be emphasized that there is a significant similarity between the nephridial structure of such Oligochaete species as *Branchiobdella*, and the Haplotaxida, and those of the Hirudinea.

Now a few words about the demarcation of the various parts of the nephridium in the Hirudinea in general.

After having examined the relevant findings of other authors and after his own investigations, GRAF (1899, p. 272) came to the following conclusion: "Dividing an organ according to its shape is thus completely useless. We must look for another principle of classification. The physiological significance of the different sectors may be well suited for such as purpose". He differentiated between "a *portio afferens* (consisting of *infundibulum* and *receptaculum excretorium*), a *portio afferens-glandulosa*, a *portio glandulosa-efferens*... a *porto efferens* (consisting of *vesicula terminalis* and *canalis terminalis*)". The present author feels that GRAF's disregard for the morphological principle is unjustified. The same 4 components can also be differentiated when the examination is made according to purely morphological characteristics. As discussed above, the structural characteristics can be quite naturally divided into 3 sectors: the funnel apparatus, the excretory nephridial sector, and the purely excretory sector, i.e. the invagination of the skin epithelium. This division is also consistent with the history of the development of nephridia (BÜRGER, 1891, 1894, 1902), although there is probably not quite enough material available in that regard. Furthermore, regarding the excretory sector as an entity, we can see a secondary differentiation into the sector with ramified tubules and the sector with a single central canal. These two sectors are of quite similar structure and cannot be compared at all with the 3 above established main categories. The present author feels that GRAF also did not have sufficient physiological reason to do this. The two just mentioned sectors together form a "*portio glandulosa*", and their sector with the ramified tubules is "*afferens*" as well as "*efferens*". This equally applies to the sector with the single central canal. In this case, GRAF himself, without realizing it, was influenced by the observed morphological characteristics of this nephridial sector, while earlier (1894, p. 165) he had far more accurately divided the nephridium into "3 sectors ... a terminal bladder, a glandular sector, and a ciliate funnel".

The sector with the single central canal could be further divided into certain zones which would differe mainly in the size of their cells and the width of the canal, but these conditions fluctuate too much to be regarded as a general phenomenon. The same applies to the position of the different nephridial parts in relation to each other. A differentiation of the nephridium into different sectors according to that position, as suggested by BOURNE or OKA, would in many cases be forced and improper. GRAF already emphasized this in the quotation cited above.

In *Acanthobdella* the fluctuations in the relative position of the nephridial parts are characterized in that the anterior and posterior nephridial legs are not behind each other: one is situated mediad, the other latarad. This characteristic is connected with the position of the adjacent organs, especially the testis.

In regard to the said ordinary positional relationships of individual parts, the two anterior pairs of nephridia ($nph_{6,7}$) show significant deviations (Fig. 33, No. 1). It is found that the nephridium begins in the 2nd (7) and 1st (6) preclitellar somite at the 2nd somite annulus, and extends caudad, while its anterior leg is resting against the medial wall, and the posterior leg is resting against the lateral wall of the lateral outpouchings of the coelom of the 3rd or 2nd somite, respectively (Fig. 33, No. 4 cs_7). By and large the legs themselves are formed in the ordinary manner. However, the part pointing dorsad and mediad is well-developed only in the nephridium of the 2nd preclitellar somite, where it ends dorsad at the transition between the coelom outpouching (Fig. 31, No. 7 cs_8) and the coelom sinus of the 3rd preclitellar somite surrounding the intestine, while in the nephridium of the 1st preclitellar somite this part is reduced and appears as a compact mas of nephridial loops: the nephridium itself thus extends only as far as the posterior limit of its somite.

In *Protoclepsis tessellata* and *Pr. maculosa* the author has observed that the nephridia of these somites have also shifted caudad. They are independent of each other and extend caudad in their somite from the excretory duct almost to where they contact the following nephridium. According to OKA (1894, p. 125) a similar characteristic is seen in the nephridia of the preclitellar somites in *Glossisiphonia complanata* and *Gl. heteroclita* of which he wrote that they are even "connected with each other".

At the end of this description a few words about the nephridium of the 3rd clitellar somite of *Acanthobdella* (Fig. 39, No. 82). As mentioned, it has a well-developed eliminating sector on which occasionally only a single cell (npz) is present at the inner end instead of the entire excretory nephridial sector. This cell is rather large and possesses a conspicuous nucleus: in its periphery can be seen the typical radially striated layer. This cell, located in the inner body mesenchyme, has no relationship with any other elements of the body except the corresponding skin invagination (ep). This is an interesting case: apparently the design of the excretory nephridial sector has stood still at its lowest level of development.

13. The reproductive organs

As all Hirudinea, *Acanthobdella* is hermaphroditic.

As far as the **male reproductive apparatus** is concerned, A. KOWALEWSKY (1896, p. 269) wrote as follows:

> „Les organes genitaux conservent le type de vrais Hirudinées avec cette difference que les testicules sont reunis dans deux organes latéraux qui se prolongent en forme de deux sacs des deux côtés du corps en commençant du 5. somite jusqu'au 15., c'est à dire jusqu'au somite dans lequel finit l'intestin median et la région mediane du corps en general. L'ouverture extérieure des organes genitaux males se trouve sur le 7. (?) somite, c'est à dire entre le 4. et 5. ganglion de la chaine ventrale; dans ce meme segment se trouve la communication de la cavité des testicules avec les canaux déférents. La difference de la structure des testicules de l'*Acanthobdella* de celle des autres Hirudinées consiste en cela que les testicules forment deux poches symétriques qui se prolongent dans la partie antérieure du corps dans deux somites plus en avant que le somite où se trouve l'ouverture genitale mâle" .... (p. 267). „Les glandes mâles sont placés dans les parois du corps et forment seulement des proéminences dans le coelome."

E. BRUMPT (1900, p. 306) also wrote very little about the male reproductive apparatus of *Acanthobdella*:

> „Cette curieuse espèce a été l'objet d'un travail détaillé du professeur Kowalevsky. Il n'existe qu'une paire de testicules qui s'étendent d'un bout à l'autre du corps sous forme de deux sacs allongés; ils se déversent dans deux canaux éjaculateurs de forme assez irrégulière qui aboutissent à une portion commune s'ouvrant directement à l'extérieur. Il n'existe ici aucune invagination épidermique (bourse) autour de l'orifice mâle, et c'est pour cela qu'il présente une forme si nettement circulaire."

This is all that has been known thus far about the male reproductive apparatus of *Acanthobdella*. By and large, the present author can confirm these findings based on his own observations.

In *Acanthobdella* the spermatogenetic part of the male reproductive apparatus is formed by 2 testes (h) embedded on each side in the inner body mesenchyme (Fig. 33, No. 1, 6; Fig. 34, No. 8-11; Fig. 40, No. 93, 96). Each testis is comprised of a sac-like structure, of usually oval cross section, extending from the boundary between the 3rd preclitellar (8) and 1st clitellar (9) to the 8th (19) somite of the midgut region, i.e. through 10 somites. Occasionally the testis does not reach that far back, ending in the 7th, 6th or 5th somite (18, 17, 16) of the midgut region or even before. It is often found that the cavity of the testis narrows in the clitellar somites; such a cavity is almost never present in the mid body somites.

The structure of the testicular wall (ct_1) cannot be distinguished from that of the parietal coelothelium (ct). It consists of a very thin membrane resting against the marginal lamella of the mesenchyme (Fig. 39, No. 83-85) with sparsely distributed protoplasmic proliferations in addition to corresponding nuclei. A more detailed description is unnecessary, since it would be identical to that of the coelothelium of the somatopleure.

The following fact indicates that the testis is a true coelothelium: in the 1st clitellar somite (9) the testicular wall (h) borders directly on the coelom of this somite which in this sector usually consists of compact strands of colothelial cells (ct*; Fig. 33, No. 6). In the middle of this somite, about half way along the intestine, the testicular wall entirely disappears over a short distance, so that the epithelium that lines the testis (ct_1) directly merges into the peritoneal epithelium of the coelothelial strands (ct*) and the cells (h_1) of these strands protrude directly into the testicular cavity (Fig. 39, No. 83-85; Fig. 40, No. 93, 94; Fig. 41, No. 106). Thus the testis of *Acanthobdella* is definitely a sector of the coelom in terms of the structure of its walls and also because a connection exists, albeit an insignificant one, with the latter.

In this respect, *Acanthobdella* differs very significantly from all other Hirudinea, in whom all traces of a connection between testes and coelom have disappeared, and the testes themselves are divided into many, usually metameric sectors. That is why the statement by KOWALEWSKY (1896, p. 270) that "les données que je possède me font voir dans la structure des ces organes le même type que nous connaissons des Hirudinées avec certaines modifications", is not justified and could at best indicate a distant relationship as far as this system is concerned. Even the ontology of the Hirudinea, as O. BÜRGER's studies (1892, 1894, 1902) indicate, does not know of any examples of testes resembling the situation in adult *Acanthobdella*, for in the other Hirudinea the testes originate from metameric coelothelial proliferations.

The testicular cavity is filled with male reproductive products in several stages of development. It is not the author's intention to describe the spermatogenesis of *Acanthobdella* in detail here, and only the most relevant facts will be discussed.

As in the other Hirudinea, the male reproductive products in the testis of an adult *Acanthobdella* are either in the growing stage or in a period of maturation, i.e. they occur as spermatocytes of the 1st or 2nd order, as spermatides or as mature spermatozoa. In the individuals examined by the author, spermatides and spermatozoa were present in small numbers, while spermatocytes in various stages of development occurred in vast quantities.

The spermatocytes of the 1st order are often freely and individually scattered throughout the entire testis (Fig. 39, No. 86). They consist of cells that are more or less round in shape, with a diameter of about 10 μ; their protoplasm forms a finely granulated layer around the spherical nucleus whose diameter is 6 μ. The nucleus is rich in chromatin and contains one nucleolus.

As mentioned above, the coelothelial cells of the peri-intestinal cell cords of the 1st clitellar somite (9) protrude into the testicular tube, and here individual cells (sz) separate from the tissue (h_1) that generates them and thus enter the testicular cavity (Fig. 39, No. 84, 85). Nowhere else in the testis can traces of such cell proliferation be observed. The coelothelial cells that separate are extremely similar to the spermatocytes of the 1st order; the only difference is that they have an ample supply of vacuolized protoplasm. However, the more distant they are from their place of origin, the less obvious this difference becomes, and the author believes that it can therefore be assumed that these cells in turn generate the spermatocytes of the 1st order.

Thus in adult *Acanthobdella*, the coelom sector directly connected with the testicular cavity seems to be a spermatogenetic zone for male reproductive products.

This characteristic is not found elswhere among adult Hirudinea and resembles the Oligochaeta to a very high degree. In comparison with the other Hirudinea, this would be a primitive characteristic.

A summary of the author's own findings shows that contrary to the other Hirudinea, in *Acanthobdella* and in the majority of the Oligochaeta the coelom is not yet completely separated from the cavity containing the male reproductive products. In *Acanthobdella*, a connection between both cavities occurs in the 1st clitellar somite, i.e. in the 9th **body**somite, counting from the 1st chaetigerous head somite. In many Oligochaeta, but especially in the Haplotaxida, Lumbriculida, etc., the body somite in question also furnishes male reproductive products. This similarity is carried even further: as described above, the spermatogenetic zone (h_1) in *Acanthobdella* consists of a coelom sector of the somite which simply protrudes into the testicular cavity (h). This zone is therefore identical, for example, with the testes of the Haplotaxida and Lumbriculida. However, the so-called testis of *Acanthobdella* which only consists of an outpouching of the coelom of the 1st clitellar somite and plays the role of a reservoir where the male reproductive products grow and mature, does not differ at all from the sperm sacs of the Oligochaeta. It is known that these sacs are also formed by coelom outpouchings extending cephalad and caudad from the somite that furnishes the male reproductive products, and in some species they run through many body somites. It would therefore be quite accurate to regard the zone in which the male reproductive products are generated in *Acanthobdella* as the testis or male reproductive gland, and the remaining sector of the described system as sperm sacs (Fig. 40, No. 93, 94).

Occasionally it is found that the spermatocytes of the 1st order (sz) form large accumulations and are very closely accumbent to each other (Fig. 39, No. 86). In the centre of each accumulation is a cell whose body measures about 60 µ in diameter and which gives off branches of much varying, often considerable size in all directions. The spermatocytes are situated around the cell body as well as on its branches. The protoplasm of this cell is finely granulated. In its centre is an almost spherical nucleus measuring about 30 µ in diameter, amply provided with chromatin granules of various sizes. This cell, which does not show signs of division, differs considerably from the surrounding spermatocytes (sz) and should by no means be regarded as the cell producing the latter. It is definitely a nutritive cell which in this case can be compared to Verson's cell in the testes of arthropods. In the other Hirudinea, however, these homologous cells do not occur, at least not in adults. The author is unable to provide details about the origin of the described giant nutritive cells. The only testicular cells they resemble are those of the sperm funnel (Fig. 39, No. 87 st*) which will be discussed below.

The spermatocytes of the 1st order (sz) distributed around the nutritive cell are in the growing stage, and it can be observed that their nuclei are more amply provided with chromatin than the free spermatocytes. The spermatocytes situated on the ends of the branches of the nutritive cell are forming small groups and separate - apparently together with the corresponding portion of the branch's protoplasm - from the remaining mass of spermatocytes (Fig. 39, No. 86). This is how the cytophores (cy) are formed which may be nothing but such separated anucleate parts of the nutritive cell, adhering to and forming a layer around the spermatocytes. It should be noted that occasionally cytophores are encountered in whose centre a nucleus is embedded which resembles that of spermatocytes of the 1st order.

The cytophores of *Acanthobdella* reach up to 20-30 µ in diameter and are quite identical to those of the other Hirudinea. Occasionally they - together with the accumbent spermatocytes - are covered on the outside by a sort of sheath formed by 1 or 2 flat cells with an oval nucleus, but such a sheath seems to be lacking in at least half the cytophores found in the testis. The nuclei of the cells with sheaths resemble those of the free spermatocytes.

All around the cytophores the maturation process of the male reproductive products takes place in the usual manner, i.e. the spermatocytes of the 1st order become spermatocytes of the 2nd order, which finally grow into spermatozoa.

The ejaculatory part of the male reproductive apparatus of *Acanthobdella* consists of 2 sectors which differ in origin (Fig. 33, No. 1; Fig. 40, No. 93, 94). The proximal sector is formed by the sperm funnel (st; Goodrich's gonostome) and the adjacent sperm duct (vd), both of which are derivates of the coelothelium. The distal sector apparently originates in the ectoderm and contains an unpaired end tube, the atrium (at) and 2 pairs of branches of the latter, the ejaculatory ducts (dc).

In the posterior sector of the 1st clitellar somite (9) and at the boundary between them and the following somite the ordinary coelothelium of the testis undergoes a significant change (Fig. 39, No. 87). Its cells suddenly change from flat structures into a cubic or cylindrical epithelium (st). The more the boundary between the two cell types protrudes as a more or less conspicuous bulge in the testicular cavity, the more this transformation is pronounced. This bulge is none other than the sperm funnel (st) which far ventrally in the posterior sector of the 1st clitellar somite directly merges into the sperm duct (vd; Fig. 33, No. 1; Fig. 40, No. 93, 94).

The latter extends caudad for a short distance in the anterior sector of the 2nd clitellar somite (10), forms several creases in the inner body mesenchyme, and slightly protrudes into the ventral coelom sinus. It is nothing but a tube that is lined with the same epithelium as the sperm funnel.

The epithelial cells of this sector vary in structure. Occasionally it is a cubic epithelium whose elements are about 12-15 μ high and wide; in other cases a cylindrical epithelium occurs whose cells reach up to 20-25 μ in height and 10-15 μ in width (Fig. 39, No. 87). Their protoplasm is finely granulated and stains very well. At the free seam of the cells very fine cilia seem to occur, but the author was unable to determine their presence with certainty. The nucleus is round or oval, of about 10 µ in diameter, or 10-12 µ high and 4 µ wide. It contains quite numerous chromatin granules of varying size.

The cells situated at the bulge of the sperm funnel (st*), which protrude far into the testicular cavity (Fig. 39, No. 87), sometimes become very considerably enlarged in size in comparison with the adjacent elements, and their nuclei also reach a considerable size. They therefore resemble the said nutritive cells of the testis of *Acanthobdella* It is difficult to determine the interrelations between these, but it seems in some cases that the greatly enlarged epithelial cells of the sperm funnel are discharged into the testicular cavity.

In the ventral sector of the sperm funnel as well as over the entire distance of the sperm duct, a layer of circular muscle cells formed by ordinary, medium- sized, spindle-shaped cells lies outside the epithelium. The contractile substance is lacking entirely over a certain distance of the periphery of the nucleate sector. Outside the muscle layer are greater or lesser accumulations of pigment fat cells which here form a kind of special layer, while they occur only in insignificant numbers in the surrounding mesenchyme.

Curving cephalad, the sperm duct merges into the corresponding ejaculatory duct (de; Fig. 33, No. 1; Fig. 40, No. 93, 94). The latter extends in the form of a rather wide tube in the anterior sector of the ventral coelom of the 2nd clitellar somite (10) over a short distance cephalad and then leads into the atrium (at) laterally and slightly from behind. The atrium consists of a bulb-like structure whose fairly narrow cavity opens to the outside via the round male pore (ø). The atrium lies in the ventral coelom sector at the boundary between the 1st (9) and 2nd (10) clitellar somite on the median line of the body.

The skin epithelium of the body merges directly into the distal atrium sector via the genital pore, and it can be seen how quickly the skin epithelium changes into atrium epithelium. Its cells become longer and wider, but the enlargement of the nuclei is particularly conspicuous. The typical epithelial elements (dz) of the atrium appear as much elongated cells which reach up to 80 µ in length and 10 µ in width (Fig. 39, No. 88). Their basal sector has a finely granulated protoplasm that stains well and has a sort of longitudinal striation that is well visible. On the other hand, the proximal sector is greatly vacuolized and thus does not stain well. It is clearly recognizable that the secretion collecting in the vacuoles is discharged into the atrium cavity. The oval or round nucleus of the cells, about 30 µ high and 20 µ wide, usually lies in the middle or basal sector; it contains numerous chromatin granules and between them 3, 4 or more quite sizeable chromatin globules.

Between such typical glandular elements (dz) are cells (ep) that are not of glandular character (Fig. 39, No. 88). These are very long, narrow, filiform elements whose nuclei quite resemble those of the skin epithelium and are embedded in an inconspicuous thickening of the cell body.

The same glandular epithelium lines the ejaculatory duct up to its union with the corresponding sperm duct.

Outside circular muscles (mf) are resting against the atrium epithelium; these are formed by ordinary muscle cells resembling the muscle cells on the sperm duct. They also extend to the ejaculatory ducts. In addition, these two sectors have longitudinal muscle fibres, albeit in very insignificant numbers.

The above description indicates that the ejaculatory sector of the male reproductive apparatus of *Acanthobdella* has very simple relationships in comparison with the other Hirudinea. Even though an atrium has developed that is certainly already homologous to the spermatophore pocket of the Hirudinea, it shows primitive traits in the differentiation of its walls and especially of the glandular elements of the latter, and in the lack of any other structures formed by the skin epithelium: this indicates that *Acanthobdella* is closely related to the Oligochaeta. The ejaculatory ducts, whose structure is identical to the atrium, are also less differentiated in comparison with the male reproductive apparatus of the other Hirudinea. As far as the special type of testis is concerned, the formation of a sperm funnel in the posterior sector of the 1st clitellar somite is fully identical to that of the Oligochaeta and very different from that found in the other Hirudinea. Finally it should be mentioned that in the general arrangement of these organs, clearly the same positional relationships apply as in the majority of Oligochaeta: the sperm funnel lies in the posterior sector of the somite generating the male reproductive products, the sperm duct perforates the dissepiment situated behind the funnel, and in the following anterior sector the ejaculatory duct leads into the atrium (Fig. 33, No. 1; Fig. 40, No. 93, 94). How closely the ejaculatory sector of the male reproductive apparatus of *Acanthobdella* resembles the corresponding organs in some Oligochaeta can best be seen from the description by F. VEJDOVSKY and A. MRAZEK (1902) of a Tubificida species, *Potamothrix moldaviensis*.

We will now discuss the **female reproductive apparatus** of *Acanthobdella*. A. KOWALEVSKY (1896, p. 270) has described it as follows:

> „Les organes genitaux femelles s'ouvrent à l'extérieur au 8. segment, et sont composes de l'ouverture extérieure qui conduit dans une poche qu'on peut comparer au vagin ou à la matrice, d'ou partent deux tres longs canaux ou tubes que nous allons appeller les ovaires. Ces deux tubes montent auparavant en haut . . . et puis descendant sous l'intestin ils se prolongent jusqu'au 13^{me} ou 14^{me} somites."

E. Brumpt (1900, p. 349) added little that was new to this description by KOWALEVSKY, when he wrote:

> „Les sacs ovariens ont la forme de deux longs rubans aplatis intimement accoles à la paroi du tube digestif, ils augmentent régulierement de largeur depuis leur extremité postérieure jusqu'à leur partie antérieure qui devient globuleuse. Les deux portions globuleuses s'unissent au niveau de l'orifice femelle. En arrière de leur point de jonction on aperçoit une masse assez volumineuse, bilobée, qui occupe environ la moitié de la longueur du segment génital femelle; il est impossible de separer cette masse des sacs ovariens avec lesquels elle fait corps."

Turning to the present author's own observations, it should be noted that the female reproductive apparatus in all *Acanthobdella* individuals examined showed virtually the same relationships in terms of their structure and in terms of the state of the reproductive products contained in them. Since the author had no comparative material to work with, it is difficult to decide to what degree these findings deviated from the traits which characterize the female reproductive apparatus in its completely developed and functioning state. Nevertheless the author feels justified to conclude that the female reproductive apparatus in the individuals he examined, while not completely mature, was certainly in a state very close to complete maturation.

As E. BRUMPT (ibid.) indicated, the female reproductive apparatus can be divided into 2 parts, the 2 ovisacs (ov) with their oviducts (ut), and a cavity (ah) resting against the latter, with an invagination of the skin epithelium (spt; Fig. 33, No. 1; Fig. 40, No. 93, 94).

The central part of this organ system is a coelom gland (cd) situated near the transition between the ventral and the middle coelom sector at the lateral coelom wall (Fig. 33, No. 1; Fig. 34, No. 9; Fig. 40, No. 92-94). It is located in the 3rd clitellar somite (11) against whose anterior dissepiment it rests almost directly; its anterior part protrudes into the upper sector of the oviduct (ut) in the shape of massive lobes; its upper part completely fills the basal portion of the ovisac (ov). Caudad and ventrad the coelom gland protrudes into the posterior cavity (ah) of the female reproductive apparatus in the form of a conspicuous mass.

In this latter part the coelom gland consists of an accumulation of cells varying greatly in size (Fig. 40, No. 92). In the middle are the larger elements: toward the periphery they become smaller, and at the margin the large cells are rarely found, while most of them here are 2-3 times smaller. This is in keeping with the fact that occasionally mitotic divisions occur in the gland. The large cells have a finely granulated protoplasm which does not stain particularly well. Their oval or roundish nuclei reach up to 15 μ in diameter; they contain numerous fairly large chromatin granules and 1 or 2 more conspicuous chromatin globules. In the peripheral elements, the round nuclei reach a diameter of up to about 5 μ; their chromatin granules are somewhat smaller than in the large cells, and usually they contain only a single chromatin globule.

The surface of the coelom gland is covered by a thin coelothelial membrane with sparsely distributed, relatively small but typical coelothelial cells (ct_1; Fig. 40, No. 92). In some places, however, the peritoneal sheath disappears, and the small cells (cz) detach from the glandular mass and drop into the posterior cavity (ah) of the female reproductive apparatus. This cavity is more or less filled with such free elements (cz) which are spherical in shape with a diameter of up to about 10 µ. Their protoplasm is finely granulated and stains less than in the elements that are still connected to the coelom gland. Typical mitoses are rarely observed in these free cells. The author feels that this description makes it apparent how much the cells resemble ordinary coelomocytes, and these two types of cells are indeed quite identical.

The anterior sector of the coelom gland (ct_1) is pointing into the lumen of the canal discharging the reproductive products; it is relatively poorly developed (Fig. 40, No. 93, 94) and consists (in the individuals examined by the author) of small cells which are identical to the corresponding elements of that part of the coelom gland that protrudes into the posterior cavity of the female reproductive apparatus.

The dorsal part (ov) of the coelom gland consists mainly of such cells; it is characterized by its considerable development (Fig. 40, No. 92-94). The more or less compact mass of its elements actually forms the entire basal sector of the ovisac on that side. Here, the large cells are present in insignificant numbers, and mitoses are relatively rare.

As mentioned, the coelom gland (cd) laterally borders directly on the inner body mesenchyme which enters the former from the front and from the side in the form of an inconspicuous intermediate layer (ms_1), thus separating the upper from the lower part of the gland. In other words, one has the impression that the coelom gland is like a process of the inner body mesenchyme (Fig. 34, No. 9; Fig. 40, No. 92).

Embedded in the latter is the nucleate sector of a very large muscle cell which resembles the dorsoventral muscles of the head region (Fig. 34, No. 9). The cross section of the nucleate sector of the cell is oval; one diameter is about 100 µ, the other 40 µ. At the periphery of the cell the contractile-fibrillar layer is interrupted: in the central protoplasm the oval nucleus is about 80 µ long and about 30 µ wide. Dorsad and ventrad of the nucleate sector, the muscle cell gives off many processes (mf) which form regular muscle fibres (Fig. 40, No. 92). The lower of these traverse the mesenchymatous intermediate layer and the cell mass of the coelom gland to the lateral wall of the sector discharging the reproductive products of the female system, the upper perforate the upper part of the gland and enter the base of the corresponding ovisac (ov).

A very similar muscle cell is opposite the said cell in the intestinal mesenchyme at the level of the lower intestinal quadrant (Fig. 34, No. 9; Fig. 40, No. 92). The ventral fibres (mf) of the same also extend through the mesenchyme lamella of the gland to the duct discharging the female reproductive products, while the dorsal fibres on their side penetrate the basal part of the ovisac (ov).

Approximately at the level where the ventral coelom sector merges into the middle sector, the ovisac ascends inside the latter almost up to the dorsal coelom sinus (Fig. 33, No. 1). As mentioned above, this sector is a thick cord formed by the small cells of the coelom gland, covered only on the outside by a thin coelothelial coating. In the axis of the cord is a more or less pronounced lumen which constitutes the lumen of the ovisac (Fig. 40, No. 92). It is well-developed in the said basal sector of the ovisac. The closer the lumen is to its base the less it is delineated, since the elements which form a real albeit not single-layered wall are arranged into a gradually thickening layer and finally turn into loose tissue in which only poorly defined cavities remain of the formerly present lumen (Fig. 40, No.

92, 93). These cavities are in open communication with the lumen of the sector discharging the female reproductive products (ut), and thus the latter is able to communicate with the lumen of the ovary (ov).

It was not possible to observe any differentiation of the elements in the basal sector of the ovisac; peripherally between them on each side extend the above mentioned bundles of muscle fibres (mf) which originate in the 2 muscle cells as described (Fig. 40, No. 92).

The author believes that these facts indicate quite plainly that this is a case of a not quite mature and functioning organ. However, as mentioned, no other stages were available for study.

The very short ascending part of the ovisac following the basal sector and extending dorsad only along the upper intestinal quadrant, has different characteristics (Fig. 33, No.1; Fig. 40, No. 93). It forms a wide tube whose inside is lined with typical cylindrical epithelium (ovp) and whose outside is covered with ordinary coelothelium (ct). Between these two layers lies a thin layer of an unstructured gelatinous substance (ms) with cells (cdz) that are identical to the elements of the basal sector of the ovisac (Fig. 39, No. 89).

The epithelial cells (ovp) of this sector are about 15-20 μ high and 10 μ wide. Their protoplasm is finely granulated and stains well. Their free cell surface is lacking any cuticular lamella or cilia. The nucleus is oval in shape, with a longitudinal diameter of about 8 μ and a width of 12-15 μ. It contains numerous very fine chromatin granules and 2-3 coarser chromatin globules.

On both sides between the two epithelial layers in the mesenchyme are bundles of longitudinal muscle fibres (mf) which form a direct continuation of the corresponding bundle of the basal sector of the ovisac (Fig. 39, No. 89).

The ovisacs (ov) then change direction (Fig. 33, No. 1; Fig. 40, No. 93) and extend horizontally through about 4 somites in the dorsal coelom sector on each side of the median line of the body above the dorsal blood vessel (Fig. 34, No. 10, 11). However, their position can vary considerably. They gradually become narrower and either end dorsally or descend into the ventral coelom sector again before coming to an end, as described by A. KOWALEVSKY (1896, p. 270).

Over its entire length the horizontal sector of the ovisac shows a very similar structure (Fig. 39, No. 90). On the inside it has a well-developed epithelial layer (ovp) that is clearly differentiated from the epithelium of the previous sector. Its cells are of cubic or usually flattened shape and have the same characteristics as the elements of the basal sector. Outside the epithelium lies a thin intermediate layer of an unstructured gelatinous substance (ms) in which a bundle of longitudinal fibres (lm) extends on each side. These form a direct continuation of the longitudinal muscles that occurred in the 2 previous sectors of the ovisacs; they become gradually thinner and extend to the end of the ovisac. Thus the entire longitudinal musculature of this organ originates in 2 muscle cells situated, as mentioned, at its basal sector. Outside the longitudinal musculature has an overlay of circular muscle fibres (rm). Each of these is formed by an ordinary, spindle-shaped muscle cell whose nucleate sector is lacking a contractile-fibrillar layer over a distance of varying length. Characteristically the nucleate sectors are distributed in the circular musculature of the ovisac, namely along 2 lines, 1 dorsal and 1 ventral, i.e. at the same distance from the two bundles of longitudinal muscle fibres.

The outer layer of this sector of the female reproductive apparatus is formed by the coelothelium (ct) which, however, deviates considerably here from the ordinary peritoneal epithelium of the somatopleure. Usually it is seen as a flat epithelium which can hardly be distinguished from the epithelial layer that lines the inside of this sector of the ovisac. Closer to the vertical sector it becomes gradually flatter until it finally turns into the typical peritoneal membrane.

Toward the posterior end of the ovisac the differentiation of its various elements is generally less obvious, and in section (Fig. 39, No. 91) only 2 completely identical layers of cubic epithelium can be seen, an outer (ct) and an inner (ovp) which deviate sideways to allow the longitudinal muscle fibres (lm) to pass through. Also amidst each of them is a small accumulation of cells very similar to the elements of the described epithelium of the ovisacs: these represent the yet undifferentiated cells of the circular musculature (rm).

The entire lumen of the horizontal sector of the ovisacs is filled with developing female reproductive products (oc); however, the author was unable to observe any mature eggs in the individuals he examined (Fig. 39, No. 90, 91). For that reason, details of ovogenesis will not be discussed here. It should only be mentioned that masses of reproductive cells are gathered around quite considerable protoplasm accumulations which assume the role of nutritive centres (nrz; Fig. 39, No. 90). The latter occasionally contain spherical nuclei measuring about 25 μ in diameter, containing numerous very fine chromatin granules and 2, 3 or more coarser chromatin globules. These nutritive cells are identical with the above described elements found in the testes.

The reproductive cells are not connected with the elements of the ovisac wall whose epithelium is always well differentiated, although both kinds of cells are of the same type.

Thus an overview of the entire structure of the ovisac shows that while in some of its sectors all wall layers consist of differently differentiated elements, others are without such a clear differentiation. Thus the posterior end of the ovisac is formed of 2 quite identical epithelial layers between which are found cell accumulations of similar character for the future circular musculature. The author feels that this fact unequivocally indicates that all described elements have a common origin. This assumption is confirmed by the fact that almost no layers can be differentiated in the structure of the basal sector of the ovisac: here a mass of quite similar cells is found which merges into the cell mass of the coelom gland. This finding also indicates with certainty that it is the coelom gland from which the ovisac has originated. The similarity of the elements and the fact that the mass of the reproductive products is fully segregated from the epithelial layer of the ovisac wall also clearly indicates that the reproductive products are of the same origin: nowhere in the ovisac wall are there places where the cells proliferate into the lumen of the ovisac. It can thus be assumed with some certainty that the elements of the coelom gland situated at the anterior dissepiment of the 3rd clitellar somite greatly proliferate and produce a solid cell cord extending upward through several somites in the peri-intestinal coelom sinus. Due to further differentiation of the elements, the wall of the ovisac is generated on one side of this cord, and the mass of female reproductive products is generated on the other side - from the centrally situated cells.

The described structural conditions of the sector generating the female reproductive products clearly show that in *Acanthobdella* this sector has characteristics that are typical for the other Hirudinea as well. This is also confirmed by the embryological data furnished by O. BÜRGER (1902) regarding the development of the ovaries in Rhynchobdellida from one pair of female gonoblasts in the 11th somite.

An important difference in comparison with the other Hirudinea is the mere presence of the coelom gland whose cells give rise to this entire sector of the female reproductive apparatus of *Acanthobdella*. In the former such a gland is lacking altogether; however in the embryonic development it is reduced to a single mesodermal female gonoblast, which is in full agreement with the teloblastic mode of development common in Hirudinea. It is necessary to note here that the situation in the Glossosiphonida is similar to that in *Acanthobdella*: a muscle bundle enters the basal sector of the ovisac from the surrounding mesenchyme. As reported by G. BRANDES (1901, p. 773) in *Hemiclepsis marginata*, and confirmed by the present author in *Protoclepsis tessellata*, this bundle then enters the at first most proximal end of the mass of female reproductive products. The similarity is even greater when BRANDES's statement (p. 772) is taken into account, that he "observed the formation of the new generative cord in the wall of the ovisacs, namely where the fibrous process occurs". However, BRANDES's statement conflicts with E. BRUMPT's findings (1900, p. 356) who observes that the proliferation of the germ cells takes place in the posterior end of the ovisac. O. BÜRGER (1902, p. 536, 537) also disagrees with BRANDES and contends that the fibrous appendages of the ovisacs represent a later stage in the development of the female reproductive apparatus.

This question remains to be answered by future researchers, but as far as *Acanthobdella* is concerned, it can be stated that due to the presence of the coelom gland the sector in which the female reproductive products are generated is related to the corresponding sector in the Oligochaeta. In the latter, the ovaries form accumulations of reproductive elements that separate and drop into the coelom. In Acanthobdella, a differentiation of the wall cells takes place in the cell cords originating in the coelom gland and situated in the coelom sinus, and thus the female reproductive products here are already enclosed in an oviduct. In the other Hirudinea, such a coelom gland is no longer present, but ontogenetically a number of mesodermal cells separate and form a cell cord which then becomes exactly as differentiated as in *Acanthobdella*.

The discharging sector of the female reproductive apparatus of *Acanthobdella* consists of a wide container formed by the union of the basal sectors of the two ovisacs, and the actual discharging duct opening to the exterior (Fig. 33, No. 1, Fig. 40, No. 93, 94 ut).

The latter (ut) consists of an invagination of the skin epithelium which, beginning at the boundary between the 3rd and 4th annulus of the 2nd clitellar somite (10), traverses the muscle layers and the inner body mesenchyme. In cross section this invagination has the shape of an oval whose greater diameter is perpendicular to the longitudinal axis of the body (Fig. 40, No. 94). The epithelium of this invagination quite resembles the skin epithelium of which it is a direct continuation. In some individuals examined by the present author, he noted a differentiation into 2 parallel tubes to the left and right of the median line, but he was unable to observe the further development of this sector of the female reproductive apparatus in these particular specimens.

At the base of this invagination the circular muscles of the integument are more developed, and some give the appearance of circular muscle fibres specific to this invagination. Over the entire length of the latter, only a few fine longitudinal muscle fibres are present; they are more sparsely distributed over the posterior than over the anterior surface. They all originate from 4 muscle cells, 2 of which are situated anterior and are identical to the muscle cells in the basal section of the ovisac; their nucleate cell sectors are symmetrically situated on both sides of the median line at the upper end of the invagination. The other 2 muscle cells are less developed: their nucleate sectors are in the inner body mesenchyme near the corresponding sector of the outer muscle cell which belongs to the basal sector of the ovisac, but slightly dorsad and laterad of the same. The muscle fibres of these two cells extend along the posterior surface of the epithelial invagination.

The said longitudinal muscle fibres are resting directly against the epithelium of the invagination and are embedded in a thin mesenchyme layer which basally merges into the inner body mesenchyme. On the posterior surface of the invagination the mesenchyme layer is very poorly developed, but anteriorly it represents at the same time the mesenchyme of the dissepiment between the 2nd and 3rd clitellar somite.

Dorsad the wall of the epithelial invagination directly merges into the wall of the vessel that is formed by the union of the two basal ovisac sectors (Fig. 40, No. 93, 94). Inside this reservoir is lined with a thin epithelial layer which closely resembles that of the horizontal ovisac sector. The mesenchyme which is resting against the outside merges directly into the peri-intestinal and inner body mesenchyme. In it are longitudinal muscle fibres, and those coming from the two anterior muscle cells of the epithelial proliferation extend upward, while the others coming from the muscle cells at the base of the ovisacs extend downward. As we have seen, the anterior part of the coelom gland separates this cavity from the lumen of the ovisacs, but this delineation is incomplete in the individuals examined by the author and is probably only due to the immature stage of the female reproductive apparatus. No doubt during further development of the still poorly differentiated basal sector of the ovisacs a tube with well-developed walls is formed here which leads directly into the lumen of the discharging sector. The author has actually observed one such case resembling this situation.

As has been noted in regard to the structure of the sector generating the female reproductive products in *Acanthobdella*, there is a similarity to the other Hirudinea. The structure of the discharging sector, too, is typical for the Hirudinea and deviates far from the characteristics found in the Oligochaeta.

Directly behind the discharging sector (ut) is the posterior cavity (ah) of the female reproductive apparatus of *Acanthobdella* (Fig. 33, No. 1; Fig. 34, No. 9; Fig. 40, No. 92-94). Its anterior wall is formed in the ventral part by the posterior wall of the said epithelial invagination (ut) which is covered only by a layer closely resembling the parietal coelothelium (Fig. 40, No. 93, 94). In the dorsal part the anterior wall is less differentiated, since it consists here of a collection of the small cells of the coelom gland (cf) traversed by the muscle fibres (Fig. 40, No. 93). The coelothelial layer is apparently developed here as well, since nucleate cell sectors can occasionally be found which are characteristic for this layer. Nevertheless it can be stated that the posterior cavity of the female reproductive apparatus is not connected with the upper part of the discharging sector, since the peritoneal lamella is not continuously formed, and the elements of the wall only form a rather loose mass. Laterad the posterior cavity of the female reproductive apparatus extends as far as the paramedian longitudinal muscle strand (Fig. 40, No. 92-94); ventrad it extends along the median line of the body to the ganglion of the ventral cord, on each side of which it forms an outpouching reaching almost to the posterior margin of the 3rd clitellar somite. Protruding anteriorly and dorsally to the right and left into the posterior cavity are the two said coelom glands (cd) whose separating elements, as mentioned, drop into this cavity which they more or less fill. The lateral and posterior wall of the cavity and the posterior sector of their upper wall are formed by typical coelothelium (ct) of the somatopleure against which relatively small, spindle-shaped muscle cells (mf*) are resting from the exterior. One end of the latter is fastened to the basal sector of the ovisacs, while the other end enters below the skin epithelium (Fig. 40, No. 92). These muscles are embedded in the inner body mesenchyme surrounding the posterior cavity. Ventrad the said cavity forms numerous outpouchings which extend as far as the circular (rm) and diagonal (dm) muscles. Occasionally these outpouchings are so well-developed that some longitudinal muscle bundles (lm*) in the posterior cavity (ah) itself are quite isolated from all other longitudinal muscles (Fig. 40, No. 92). Here, the coelothelial lining of the posterior cavity undergoes a peculiar change which is to a certain degree analogous to the chloragogen cell layer of the intestine: rather large, oval or pear-shaped cells (ct*) occur here and reach approximately up to 30 µ in height and 15 µ in width. With such cells the outpouchings of the posterior cavity which enter between the longitudinal muscles are densely packed. Their protoplasm is finely granulated and stains faintly. The oval or spherical nuclei measure about 15 µ in diameter and are provided with very fine chromatin granules and 3, 4 or more chromatin globules. These cells resemble the elements in the wall of the ascending part of the ovisacs.

Characteristic for the posterior cavity of the female reproductive apparatus of *Acanthobdella* is the invagination (spt) of the skin epithelium that protrudes toward it (Fig. 33, No. 1; Fig. 34, No. 9; Fig. 40, No. 92, 93). Beginning at the boundary between the 2nd (10) and 3rd (11) clitellar somite, it extends in the form of a flat but wide depression below the anterior sector of the posterior cavity. At its bottom the ends (mf_1) of the ventral dissepiment muscles (dsz_1) attach themselves; there are 2 of these on each side as usual (Fig. 34, No. 9; Fig. 40, No. 92). The other ends of the latter turn toward the corresponding ventral quadrant of the intestinal sector and run close to the inner muscle cells of the basal ovisac sector. Their middle parts protrude into the posterior cavity of the female reproductive apparatus on the median line of the body between the two coelom glands. The tissue (ms) separating the cavity from the invagination of the skin epithelium looks like an extremely loose, easily penetrated mesenchyme provided with many amoebocytes (Fig. 40, No. 92).

E. BRUMPT (1900, p. 370) wrote that the posterior cavity of *Acanthobdella* "se présente une simple hypertrophie de la paroi postérieure de l'oviducte, la masse ainsi formée est creusée à son centre d'une volumineuse lacune dont la paroi postérieure et supérieure est extrémement délicate, surtout sur la ligne médiane". Yet because of the presence of a clearly developed coelothelium (ct) which is ventrally (ct*) changed, but otherwise identical to the somatopleure, the posterior cavity of the female reproductive apparatus must not be regarded as a lacunar space. On the contrary, it is apparently a separate coelom sector with a distinctive function having to do with the reproductive apparatus. Furthermore, BRUMPT's view of the posterior cavity of the female reproductive apparatus as a structure representing a simple hypertrophy of the posterior wall of the oviduct is quite inaccurate because the coelom glands - which could indeed give this impression - are clearly delineated from the rest of the wall of the said cavity, and since the wall itself is largely formed by the typical coelothelium of the somatopleure. As far as *Acanthobdella* is concerned, BRUMPT was apparently influenced by the results which he obtained in his detailed examination of the reproductive apparatus of the other *Hirudinea*.

In spite of this inaccurate description by BRUMPT, his findings (1900, p. 349) that "l'orifice énigmatique de GRUBE n'est pas un orifice, ce n'est qu'une simple dépression, profonde il est vrai ... une aire copulatrice" and "la glande qui adhère intimement au fond de cette dépression ... n'est autre chose que le tissu vecteur des autres Ichthyobdellides" are quite correct. Indeed in its location and its relationships to the other body parts, the invagination of the skin epithelium of *Acanthobdella* completely corresponds to the copulatory region described by BRUMPT in the other Ichthyobdellida. In many species, the vector tissue is also directly connected with the female reproductive apparatus, as the present author has observed in the posterior cavity of *Acanthobdella*. BRUMPT (1900, p. 349) wrote as follows in this regard: "Les coupes que nous avons pratiqués chez des animaux fixés longtemps après la reproduction ne nous ont pas montré la présence de spermatozoïdes dans ces tissus mais l'anatomie comparée ne nous permet pas de garder des doutes à cet égard", i.e. that *Acanthobdella* has a copulatory region and a vector tissue homologous to the Ichthyobdellida. Yet we should not place *Acanthobdella*, as BRUMPT wishes to do on the basis of his not quite accurate observations, in the same group with *Piscicola geometra*, *Cystobranchus respirans*, *C. fasciatus*, and *Trachelobdella* sp. The said formations in *Acanthobdella* are much more primitive than those in all other Hirudinea. While in the latter, the copulatory region reaches fairly sizeable dimensions, in *Acanthobdella* it is localized in a small area , and the vector tissue of the Ichthyobdellia consists of a mass interspersed with lacunar spaces, while in *Acanthobdella* it is still recognizable as a typical coelom sector. In the author's opinion, this latter fact is a clear indication that we are facing a primitive state that represents an intermediate stage between the Oligochaeta and the Hirudinea. The Oligochaeta have no such differentiated coelom sector as the posterior cavity of the female reproductive apparatus in *Acanthobdella*, which only occurs in the latter. In the Ichthyobdellida, on the other hand, the posterior cavity has already been replaced by a special tissue designed to enable the spermatozoa to reach the female reproductive products from the spermatophores. The same role is apparently played by the posterior cavity of the female reproductive apparatus of *Acanthobdella*, where the spermatozoa can easily penetrate through the invagination in the skin epithelium. This invagination would therefore play the role of a place specialized for the penetration of the spermatozoa, which is confirmed by the above described structure of the invagination. Formations of a similar structure in the Oligochaeta are the spermathecae which also are nothing but invaginations of the skin epithelium, sometimes situated on the ventral median line of the body.

The general topographic relationships of the female reproductive apparatus of *Acanthobdella* can be summarized as follows: On each side of the anterior sector of the 3rd clitellar somite, i.e. the 11th body somite, counting from the 1st chaetigerous head somite, is a coelom gland that is homologous to the ovaries of the Oligochaeta. The discharging sector of the reproductive apparatus lies directly at the anterior dissepiment of the same somite. The external opening, however, is in the furrow between the 3rd and 4th annulus of the 2nd clitellar somite, i.e. it has undergone a slight anterior displacement. One annulus further caudad, on the median line of the body, is a spermatheca with a differentiated coelom sinus situated ventrally in the 3rd clitellar somite. Thus the 3rd clitellar (i.e. the 11th body) somite of *Acanthobdella* should be regarded as the female reproductive somite of this species.

In *Acanthobdella*, it is possible to determine the 1st clitellar (9th body) somite as the male somite, and the 3rd clitellar (11th body) somite as the female somite. These relationships are not nearly as simple in the other Hirudinea, especially in fully mature adults. However, embryological facts can be used to clarify the situation in this case, too. Thus it can be stated with certainty that the 11th body somite constitutes the female somite in the other Hirudinea, as it does in *Acanthobdella*. In regard to *Glossosiphonia*, O. BÜRGER (1902, p. 536) wrote: "The female reproductive organs with all their accessories are generated by the products of the gonoblasts of the 11th segment". He was just as certain that the ejaculatory sector of the male reproductive apparatus in the other Hirudinea belonged to the dissepiment between the 9th and 10th body somite, just as in *Acanthobdella*. The relevant finding of O. BÜRGER (1902, p. 537) regarding *Glossosiphonia* was as follows: "The male reproductive organs have their origin in two different areas. Only the seminal vesicle and the ejaculatory duct, the spermatophore pouch and the unpaired discharge duct are produced

TRANSLATION NOT EDITED FOR PUBLICATION.
TRADUCTION NON DESTINEE A LA PUBLICATION

by the pair of gonoblasts in the 10th segment", where they are situated in the region of the dissepiment betwen the 9th and 10th somite. This indicates the probability that the 10th body somite in *Acanthobdella* as well as in the other Hirudinea represents neither the male somite nor indeed any reproductive somite, and that the male reproductive products must enter the 9th body somite before reaching the discharge duct. Thus the 9th somite should be regarded as the actual male reproductive somite. The homologies between the reproductive apparatus of *Acanthobdella* and that of the other Hirudinea do not go any further, since the spermatogenetic sector of the male reproductive organs in the latter has quite peculiar characteristics, deviating considerably from those in *Acanthobdella* and the Oligochaeta, in that it is formed of thickenings in the coelom wall of somites in the midgut region.

The author wishes to draw attention to the fact that in all Hirudinea, similar to *Acanthobdella*, 3 somites play the role of clitellar somites, namely the 9th, 10th and 11th counting from the 1st somite innervated by the subesophageal ganglion mass. A consistent position of the genital pores in certain clitellar somites, as some authors claim, for example S. APATHY (1888), A. OKA (1894), and R. BLANCHARD, can in the present author's opinion not be observed in the Hirudinea. Even the Glossosiphonida contain such opposite species as *Glossosiphonia heteroclita* on the one hand, and *Protoclepsis mollissima* on the other. While in the former the male and female discharge ducts of the reproductive apparatus lead to the outside in a common opening situated between the 1st and 2nd annulus of the 10th body somite, i.e. the 2nd clitellar somite, in the latter the male genital pore lies in the 9th body somite, i.e. in the 1st clitellar somite between its 2nd and 3rd annulus, the female pore, however, between the 1st and 2nd annulus of the 3rd clitellar somite, in other words in the 11th body somite. This shows that it is extremely difficult if not impossible to use these characteristics for a comparison with *Acanthobdella*.

The above has shown how closely the various parts of the reproductive apparatus of *Acanthobdella* are related to those of the Oligochaeta. It is easy to see that the positional relationships are also very similar to those in certain Oligochaeta. A look at the Haplotaxida, for example, shows that their testes are situated in the 9th and 10th chaetigerous somite and the ovaries in the 11th and 12th or only in the 11th somite. There is very little difference between those traits and those found in *Acanthobdella*. *Branchiobdella* is an intermediate link in this relationship, since in this genus a somite lies between the male and female somites which is lacking reproductive products. An important factor in the present case is the occurrence of a somite at all in which the reproductive organs have atrophied, quite apart from the fact that the position of the reproductive somites is different than in *Acanthobdella*. Such a retrogressive development has probably also taken place in the latter species in the 2nd clitellar, i.e. 10th body somite. As noted above, the structure of the discharging sector of the male reproductive apparatus fully resembles that in some Oligochaeta and is very closely related to that in the Haplotaxida. There is a difference in the position of the spermatheca, but that organ is subject to very considerable fluctuations in the Oligochaeta. For example, in some Lumbriculida species the spermathecae are either before or behind the reproductive somites, or they can be in the reproductive somites themselves as is in *Acanthobdella*. It is quite understandable that the spermatheca has shifted into the immediate vicinity of the discharging sector of the female reproductive apparatus to ensure that the spermatozoa have access to the female reproductive products, and the separation of the posterior cavity of the female reproductive apparatus from the remaining coelom serves the same purpose. A certain peculiarity of *Acanthobdella* in comparison with the Oligochaeta is that that it is difficult to determine whether the female discharging duct is homologous to the oviducts of the Haplotaxida or whether it is closer related to the sperm ducts of the 2nd pair of testes; it is conceivable that after the retrogressive development of the latter the corresponding sperm ducts have assumed the function of discharging the female reproductive products.

Summarizing the above, it can be concluded that the reproductive apparatus of *Acanthobdella* constitutes an intermediate type: the structure of the male reproductive organs is closer to that of the Oligochaeta, while the female organs are closer to those in the other Hirudinea. In this regard as well from other points of view, *Acanthobdella* provides us with very valuable information about the organization of Hirudinea and about the general body structure of the latter in comparison with other annelids.

14. The somite of *Acanthobdella*

At the end of our discussion about the factual material provided by the organization of Acanthobdella, we must mention some characteristics of its external morphology that have thus far not been compared with some other analogous facts.

Thus we were able to conclude that the typical mid body somite of *Acanthobdella* shows a clearly defined annulation, as is characteristic for somites of Hirudinea in general. Judging by the structure of the nervous system and the distribution of the sensory organs, it can further be in most Rhynchobdellida and to the two anterior somite annuli of the Gnathobdellida

concluded that the 4 annuli forming each somite of *Acanthobdella* are strictly the equivalent of the somite annuli in the other Hirudinea. The 1st annulus is homologous to the 3 most anterior somite annuli together in most Rhynchobdellida; the 2nd annulus is the equivalent of the middle somite annulus in the other Hirudinea, and the 2 posterior annuli of the somite of *Acanthobdella* together correspond to the 3rd somite annulus of the Rhynchobdellida and the 4th and 5th annuli of the somite in the Gnathobdellida.

The presence of a very characteristic Hirudinean type annulation in the somite of *Acanthobdella* seems to provide an important indication that a similar annulation must have existed already in the most primitive Hirudinean species. There have probably never been true Hirudinean species whose somite consisted of only one annulus. This is confirmed by the occurrence of a well-developed annulation in the somite of the nearest relative of the Hirudinea among the Oligochaeta, namely in *Branchiobdella*, in the Haplotaxida and the Lumbriculida. The author has already presented his views on this subject earlier (LIVANOW, 1904, 2).

We will now examine the reduction of the typical somite of *Acanthobdella* in the anterior and posterior ends of the body. First of all it should be noted that the most important components of the neurosomite are completely developed in all reduced somites, a fact that is confirmed by the author's observations in the other Hirudinea. The only exception are the 4 somites of the attachment disk region which have fused so closely together that it is no longer possible to find any kind of separation. But otherwise, 4 caudal somites of the hindgut region are subject to reduction in the posterior body sector of *Acanthobdella*. In all these, the middle annular furrow is well-developed, while the anterior furrow is less developed, and the posterior furrow can now only be observed on the dorsal side.

An analogous situation is found in the somites of the head region. Here the middle furrow that occurs in the 3rd, 4th and 5th head somites proves to be the most constant. A poorly developed anterior and posterior annular furrow can only be observed in the 4th and 5th head somites, and ventrally it disappears completely. In the 5th head somite the posterior furrow is usually already well-developed. The 1st and 2nd somites of the head region each contain only one annulus.

It can therefore be concluded that in the somite reduction process of *Acanthobdella* the middle annular furrow of the somite is retained the longest, and that in comparison with it, the anterior and posterior furrows are far less constant. This means that the middle furrow that separates the anterior, mostly sensory sector of the somite from the posterior sector also constitutes phylogenetically the more constant, earlier acquisition of the somite that originally had only 1 annulus. Probably even the most primitive Hirudinean species had such a biannular somite. It should be noted that quite analogous conditions are found in the somite reduction of the other Hirudinea. The presence of 2 annuli in the somite of *Microbdella* should also be regarded as an analogous development. Another important indicator in this regard is the presence of 2 annuli in the somite of *Branchiobdella*, in many Haplotaxida and Lumbriculida, i.e. in those Oligochaeta that are the closest relatives of the Hirudinea. In his earlier studies (LIVANOW, 1904, 2) the present author has already discussed the views of other researchers in detail, and it should only be noted here that almost all have more or less recognized the phylogenetic importance of this biannular somite.

It should still be explained that we have been able to confirm with absolute certainty that the body of *Acanthobdella* consists of 29 somites, 5 of which participate in the composition of the head region, while 6 belong to the preclitellar and clitellar region, 8 to the midgut region, 6 to the hindgut region, and 4 to the attachment disk region. The other Hirudinea consistently have a total of 32 body somites. This difference is due to the uneven number of somites constituting the attachment disk region. In the other Hirudinea their number is 7, while *Acanthobdella* has only 4, as mentioned. This fact is easy to explain, considering that in the other Oligochaeta the new development of somites in the posterior end of the body is a very comon occurrence. This also explains the lesser differentiation and development of somites in this body region. It is therefore obvious that a difference in the number of somites is most likely to occur in the posterior end of the body, i.e. in the case of Hirudinea in the attachment disk region.

Thus P. MOORE's conclusion (1900, p. 55) applies only to *Acanthobdella* and not at all to the various genera of Gnathobdellida and Rhynchobdellida. MOORE wrote: "On the other hand, it is even more probable that the process of reduction of the number of somites below that found in primitive annelids may have continued after the establishment of the Hirudinean type, and have progressed further in some forms than in others".

When we assume that the total number of body somites in Gnathobdellida and Rhynchobdellida is always 32, this seems to bring us into conflict with the findings of other authors. Thus C. WHITMAN (1892) counted 34 somites in the body of *Glossosiphonia hollensis* WHITM., and later C. BRISTOL (1898), P. MOORE (1900) and W. CASTLE (1900) concluded that many Hirudinean species also had 34 somites. However, this is only an apparent contradiction, since all these author have made the same mistake. As mentioned, they mistook the cephalic lobe innervated by the supraesophageal ganglion mass for 2 ordinary, much reduced somites. As the present author has demonstrated above, this view is untenable. Therefore if the 2 extra somites are deducted from the said 34 somites assumed by the above authors, the actual remaining number is 32. Disregarding the findings of R. BLANCHARD and A. OKA (1894), which are insufficient in terms of this question, we will now examine the relevant observations of S. APATHY (1888) in some detail.

APATHY claimed that the Hirudinean body consists of 33 somites, the 6 anterior of which form the head region and are innervated by the 6 ganglia forming the esophageal ganglion masses. However, as just mentioned, the 2 presumed rostral somites are none other than the cephalic lobe, leaving only 4 somites for the head region. The present author (LIVANOW, 1900, 2) has therefore attributed to the head region of Hirudinea 4 somites and the body sector innervated by the supraesophageal ganglion mass. A detailed examination of the organization of *Acanthobdella*, on the other hand, makes it apparent that the head region of this form consists not of 4, but of 5 almost identical somites: all have a well-developed chaetal apparatus, and they are without nephridia. The union of their numerous ganglion masses is of no importance, since each of the ganglia have maintained their individuality. In the other Hirudinea the situation is very similar: unlike the following somites, the 5 most anterior somites are also lacking nephridia; the associated ganglia retain their individuality even in the subesophageal ganglion mass. The development of the anterior sucker does not change the fact that this organ is formed exclusively at the expense of the 2 most anterior head somites and that the 3rd somite of the head region constitutes its most posterior labium. Thus in regard to the anterior sucker, the 4th and 5th head somites show very similar characteristics. Based on that, the author feels that the head region of the Hirudinea should include not 4 but the 5 most anterior body somites. It should be noted that strangely enough APATHY apparently disregarded the last somite of the head region completely, and it is therefore not included in the total number of somites he accounted for.

The 6 somites following the head region were regarded by S. APATHY as the clitellar region in which he differentiated the 3 anterior somites as preclitellar and the 3 posterior somites as clitellar. The latter are certainly well characterized by their close affiliation with the reproductive apparatus. The first 3 on the other hand are fairly undistinguished, and in most Hirudinea they differ from the head somites only in that they possess more or less well-developed nephridia. While the present author accepts this classification by APATHY, it should be emphasized that the preclitellar somites can justifiably regarded as a separate body region as distinctive as the actual clitellar region.

The clitellar somites are followed by the typically formed somites of the mid body. APATHY included the 6 most anterior somites in the midgut region, the 6 following somites in the hindgut region. Here it is indeed the structure of the intestine that determines the character of the somites, and the present author has therefore kept the regions as suggested by APATHY, except that their respective range had to be changed. In *Acanthobdella*, the midgut extends through 8 somites, and it is therefore quite natural to combine these 8 completely identical somites into one body region. The hindgut occupies the 6 following somites which are also identical to each other and thus together form a separate body region. Behind these somites is the attachment disk. As we have seen above, these somites are so closely fused that no demarcation between them can be found. However, taking into account the structure of the central nervous system and the distribution of the blood vessels, the present author was able to conclude that the attachment disk region is formed by the 4 most posterior body somites.

It is now generally recognized that in the other Hirudinea 7 somites participate in the formation of the attachment disk and that these somites are fused to such an extent that their individuality has completely disappeared. That is why the attachment disk region appears to be sharply differentiated from the previous region, with a clear demarcation, and APATHY was mistaken when he differentiated only 6 somites in the former. A correction of this error would mean that the anal region between the attachment disk and hindgut region consists of only 2 somites, and not 3 as APATHY concluded. In *Acanthobdella* such a region is completely lacking. In this form, the endgut only consists of an inconspicuous invagination of the skin epithelium and does not affect the character of the accumbent somites. The latter, namely the 4th and 5th somites of the hindgut region, are quite similar to the other adjacent somites.

Although we are able to determine with certainty the relationships between midgut, hindgut and endgut and the corresponding body somites in *Acanthobdella*, these are not as clearly defined in the other Hirudinea. In this respect the literature does not contain any definitive data, and we can only assume with a degree of certainty that here, too, a forward shift of the hindgut has taken place. This process would have masked the true boundaries of the hindgut region, leading APATHY to conclude the presence of a separate "anal" region, which in fact probably does not exist at all. This would mean that the situation in the other Hirudinea is the same as that which the present author found in *Acanthobdella*, namely that the midgut and hindgut regions together have 14 somites whose distribution in one or the other body region remains insufficiently determined, although judging by the analogy in *Acanthobdella*, the 8 anterior somites probably form the midgut region and the 6 posterior somites the hindgut region.

The phylogenetic relationships of Hirudinea in general and *Acanthobdella* in particular

Disregarding the view that the Hirudinea and the Platyhelminthes are directly related, which is now only of historical interest, the author will attempt - on the basis of his findings - to characterize the Hirudinea in comparison with the typical Chaetopoda

However, it should be noted that all authors agree completely in regard to the position occupied by the Hirudinea within the phylum of annelids. In their anatomical structure as well as ontogenetically the Hirudinea are the closest relatives of the Oligochaeta, forming an order which is as well-defined as the latter.

However, as seen above, *Acanthobdella* very considerably weakens this sharp differentiation between the Hirudinea and the Oligochaeta and allows us to bring the Hirudinea into a closer genetic relationship with some Oligochaete families, namely the Discodrilida and the Haplotaxida.

The body of Hirudinea consists of a certain number of somites (namely 32 except for *Acanthobdella* which has 29), and the cephalic lobe (atrophied in *Acanthobdella*). The mid body somite has a well-developed secondary annulation that is limited to the upper skin layers. In their anterior and posterior body ends the somites usually have a reduced number of annuli due to the general disappearance of annular furrows. The final result of this reduction is the somite consisting of only one annulus. Chaetae are lacking (except in the 5 most anterior somites of *Acanthobdella*). The anterior end of the body consists of a more or less developed attachment disk formed at the expense of the 3 most anterior somites and the cephalic lobe; this attachment disk is only faintly developed in *Acanthobdella* The most posterior body somites (namely 7, but only 4 in *Acanthobdella*) have completely fused to form a well-delineated and developed (in *Acanthobdella* faintly delineated) attachment disk (except in some Herpobdellida) which causes the anal opening to lie in the dorsal median line anterior to the attachment disk region. The body wall contains a circular, a diagonal and a longitudinal muscle layer. The longitudinal muscle fibres are arranged into well-developed longitudinal muscle strands (only in *Acanthobdella* are these relatively insignificant). The musculature is characterized by the special structural type of its cells (only *Acanthobdella* has some muscle fibres of Oligochaete type). The nervous system, which consists of the non-metameric supraesophageal ganglion mass and a number of ganglia (depending on the number of somites) of the ventral cord, is always completely separate from the integument. Its anterior and posterior sectors have shifted slightly toward the middle of the body; the 4 most anterior ventral ganglia form a subesophageal ganglion mass, and some (namely 7, in *Acanthobdella* only 4) of the most posterior ganglia are combined into an anal ganglion mass. The ganglia and connectives are sharply differentiated. The ganglion cells are grouped into separate follicles whose sheaths originate in single glia cells. Each ganglion contains 6 such follicles. The connectives contain 2 completely segregated thick lateral trunks and 1 small, poorly developed middle trunk known as Faivre's median nerve. In each somite the peripheral nervous system consists of 2 motoric ring nerves (an anterior and a posterior), between these extend 2 median sensory nerves, a ventral nerve and a (hardly developed in *Acanthobdella* alone) dorsal nerve. There is no lateral nerve except in *Acanthobdella*. The sensory organs protrude far below the skin epithelium and are arranged mainly in the middle somite sector; they constitute the sensory papillae and the sensilla. Through differentiation of the the retinal cells in the latter and the formation of a pigment cup, eyes are formed. Numerous gland cells enter the mesenchyme from the skin epithelium. A particularly thick development of the mesenchyme takes place in the body wall below the muscle layers (the inner body mesenchyme) and in the dissepiments. Due to this development of the mesenchyme, the central coelom sector is greatly reduced and is represented only by the dorsal (lacking in some Gnathobdellida) and ventral coelom sinus and by connecting lacunae (in *Acanthobdella* alone a regular, metamerically-arranged coelom has been retained). Instead a thick peripheral and subcutaneous coelom sector has developed (still lacking in *Acanthobdella*). The blood vascular system is completely closed and consists of a blood sinus in the wall of the hindgut and of a dorsal and a ventral blood vessel, connected anteriorly by 5 pairs of lateral vessels and posteriorly by several such vessels. (An exception are the Gnathobdellida whose blood vascular system has been completely reduced and replaced by particularly well-developed lateral coelom sectors running in longitudinal direction; here the coelom has assumed all functions of the blood vascular system). The wall of the ventral blood vessel contains longitudinal muscle fibres along its entire length, while the dorsal blood vessel has only circular muscle fibres, also only in its anterior sector. The entodermal intestinal sector is divided into midgut and hindgut whose walls always contain 2 muscle layers (circular muscles outside, longitudinal muscles inside). Th foregut consists of a pharynx with secretory ducts and a muscular esophagus. (In some Rhynchobdellida the foregut has developed into a proboscis; in many Gnathobdellida the pharynx forms jaws). Nephridia can occur beginning in the 6th body somite (except in Ichtyobdellida); they are arranged in strict metameric order (again except in some Ichthyobdellida). Their excretory sector, which is completely closed toward the coelom, is without ciliation. The sometimes lacking apparatus of the ciliate funnel has no anatomical connection with the excretory nephridial sector. The male reproductive apparatus consists of metameric testes situated in the mid body (except in *Acanthobdella* where the male reproductive gland is in the 9th body somite, but where the so-called testes form a non-metameric sac on each side), and of paired discharge ducts ending in an unpaired sector situated on the ventral median line. The main part of the female reproductive apparatus is formed by characteristic ovisacs originating in the 11th somite. The 10th body somite is not specifically related to the reproductive organs.

The above summary of the general characteristics of the body structure of Hirudinea indicates that the following traits are of particular taxonomic value as far as this class is concerned:

1. the secondary annulation of the somite;
2. the development of attachment disks at the expense of some body somites;
3. the typical structure of the muscle cells;
4. the extremely strong development of the mesenchyme;
5. (in connection with 4) the reduction of the coelom and the

development of a peripheral and subcutaneous coelom;

6. the differentiation of the ganglion cell follicles in the central nervous system;
7. the differentiation of the entodermal intestinal sector in the midgut and hindgut;
8. nephridia that are closed toward the coelom, and the absence of ciliation in their excretory sector, also the anatomical independence of the funnel apparatus from the excretory sector;
9. the development of ovisacs in the female reproductive apparatus.

It is the presence of these main characteristics (which, of course, may be developed to a varying degree) that determines whether a certain species should be included in the class of Hirudinea or not.

Acanthobdella possesses all these peculiarities, but as has been demonstrated, their development sometimes takes highly individual forms, providing us with valuable information about the manner in which these special characteristics might have evolved from the structure found in the annelids in general and in the Oligochaeta in particular.

Thus the anterior attachment disk is only rudimentarily developed in *Acanthobdella*, where this organ is at its most primitive stage of evolution: the ventral body surface here is shortened and flattened, sometimes even concave; the dorsoventral muscle fibres are present in very large numbers. The posterior attachment disk is slightly delineated from the rest of the body and lies in the longitudinal axis of the body, so that its concavity is situated in the lateral plane of the body. The structural type of the muscle cells seems to be more primitive, since the contractile-fibrillar layer at the periphery of the nucleate cell sector usually remains inconsistent, and a few muscle fibres of a well-developed Oligochaete type are present as well. Although the inner body mesenchyme is well-developed, the dissepiments are not particularly thick; for that reason the coelom around the intestine is divided into typical metameric chambers, and subcutaneous coelom outpouchings are still lacking completely. The ovisacs are formed by an outgrowth of a part of the primitive coelom gland which in the other Hirudinea has entirely diappeared.

In addition to the just enumerated most important primitive characteristics of *Acanthobdella*, the organization of this form includes some other peculiarities which have already been discussed and which represent ancestral traits in comparison with the other Hirudinea.

Apart from these, of course, *Acanthobdella* also possesses a number of specific characteristics that must be regarded as the result of its special ecological conditions. This category of characteristics includes: the complete reduction of the cephalic lobe, a body consisting of only 29 somites, an attachment disk consisting of 4 somites, and - associated with this - an anal ganglion mass consisting of only 4 fused ganglia of the ventral cord. Other specific peculiarities of *Acanthobdella* are the ring-shaped blood vessel of the attachment disk, and the formation of the entire diagonal musculature of a body somite at the expense of only 2 laterally situated cells.

On the other hand, as a form that has branched off from the common Hirudinean ancestry at a very early stage, *Acanthobdella* still has some structural traits which the other Hirudinea have already lost, while they are well-developed in the Oligochaetes for which they are characteristic. These peculiarities in the organization of *Acanthobdella* are of particular value in exploring the relationships between the Hirudinea and the Oligochaeta. They are: the presence in the 5 most anterior body somites of ventral and lateral pairs of chaetae of the type found in *Haplotaxis gordioides*; the presence of the lateral nerve, the retention of several typical relationships of the coelom which surrounds the intestine in the form of several sinuses (with the coelothelium on the intestine having been converted into a layer of chloragogen cells), and finally the continuity of the coelom with the male reproductive apparatus in the 9th body somite where the male reproductive gland is situated in the respective coelom sector and where the so-called testes begin (which are actually only sperm sacs). Another feature is the presence of a typical sperm funnel in the 9th body somite and the development of an albeit poorly developed spermatheca in the 11th somite.

All these facts provide us with sufficient evidence to establish for *Acanthobdella* a special group called Acanthobdellea that would be the equivalent of the other Hirudinean groups, the Rhynchobdellea and the Gnathobdellea. This group contains a single family, the Acanthobdellidae, with the single genus *Acanthobdella*

There are not enough reasons for combining the Acanthobdellids with the Discodrilida or for that matter to include the latter in the Hirudinea. The absence of the characteristically Hirudinean mesenchyme and thus the typically Oligochaete coelom development, the nephridia provided with a ciliate funnel opening into the coelom and with cilia in the excretory sector, the structure of the male and female reproductive apparatus all force us to regard the Discodrilida as true Oligochaetes. However, among the Oligochaetes the Discodrilida form a family which is certainly closest to those forms which must have also been the ancestors of the Hirudinea. They have a well-developed biannular somite, chaetae are completely absent.

They have an attachment disk composed of the most posterior body somites; between their circular and longitudinal muscles are diagonal muscles; the ganglia of the ventral cord contain well-developed lateral ganglion cell follicles; the intestinal musculature consists of an external circular and an internal longitudinal muscle layer; the structure of their muscle cells deviates from the Oligochaete type and approaches the Hirudinean type.

In contrast to the other Oligochaetes, the 2 latter characteristics are also typical for the Haplotaxida, a family which many authors have recognized as one of the most aboriginal of all Oligochaetes.

In closing I wish to thank my revered teacher, Professor Dr. E.. MEYER, for his constant encouragement and for the interest he has shown in my work, and for reviewing my manuscript.

Literature cited

(Titles marked * were only known to the author through other references.)

1. Apáthy, St., 1888, Analyse der äußern Körperform der Hirudineen, in: Mitth. zool. Stat. Neapel, Vol. 8.

2. —, 1897, Das leitende Element des Nervensystems und seine topographischen Beziehungen zu den Zellen, ibid., Vol. 12.

3. —, 1901, Die drei verschiedenen Formen von Lichtzellen bei Hirudineen, in: Verh. 5 internation. Zool.-Congress (Berlin), 1902.

4. Bayer, E., 1898, Hypodermis und neue Hautsinnesorgane der Rhynchobdelliden, in: Z. wiss. Zool., Vol. 64.

Beddard, F., 1895, A monograph of the order of Oligochaeta, Oxford.

5. Bergh, R. S., 1885, 1. Die Metamorphose von Aulastoma gulo, in: Arb. zool.-zoot. Inst. Würzburg, Vol. 7.

6. —, 1885, 2. Ueber die Metamorphose von Nephelis, in: Z. wiss. Zool., Vol. 41.

Blanchard, R., 1894, Hirudinées de l'Italie continentale et insulaire, in: Boll. Mus. zool. Torino, Vol. 9, No. 192.

de Bock, M., 1901, Observations anatomiques et histologiques sur les Oligochètes, spécialement sur leur système musculaire, in: Rev. Suisse Zool., Vol. 9.

Bolsius, H., 1890, Recherches sur la structure des organes segmentaires des Hirudinées, in: Cellule, Vol. 5.

—, 1891, 1. Nouvelles recherches sur la structure des organes segmentaires des Hirudinées, ibid., Vol. 7.

—, 1891, 2. Les organes ciliés des Hirudinées, ibid.

—, 1896*, Les néphridies dans les Hirudinées portent-elles un entonnoir à l'extremité intérieure? in: CR. 3. Congr. internat. Zool. (Leyde).

7. Bortolotti, C., 1902, Nota preventiva sulla funzione delle cellule chloragogene nei gen. Lumbricus ed Allolobophora, in: Atti Accad. Lincei, Rend. (5), Vol. 11, Sem. 1.

Bourne, A. G., 1884, Contributions to the anatomy of the Hirudinea, in: Quart. Journ. microsc. Sc., Vol. 24.

—, 1893, The nephridia of Leeches, ibid., Vol. 34.

8. Brandes, G., 1901, in: Leuckart, Die Parasiten des Menschen, 2. Aufl., Vol. 1, Lief. 6, Leipzig.

Bristol, C., 1898, The metamerism of Nephelis, in: Journ. Morphol., Vol. 15.

Brumpt, É., 1900, Reproduction des Hirudinées, in: Mem. Soc. zool. France, Vol. 13.

9. Bürger, O., 1891, Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von Nephelis, in: Zool. Jahrb., Vol. 4, Anat.

10. —, 1894, 1. Neue Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von Hirudo medicinalis und Aulastomum gulo, in: Z. wiss. Zool., Vol. 58.

11. —, 1894, 2. Ueber die Excretionsorgane, das Coelom und die Blutgefäße der Hirudineen, in: Zool. Ctrbl., Jg. 1, No. 17 18.

12. —, 1902, Weitere Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von Clepsine, in: Z. wiss. Zool., Vol. 72.

Castle, W., 1900, Some North American freshwater Rhynchobdellidae and their parasites, in: Bull. Mus. comp. Zool. Harvard College, Vol. 36, No. 2.

Cuénot, L., 1891, Études sur le sang et les glandes lymphatiques dans la série animale, in: Arch. Zool. exp. (2), Vol. 9.

—, 1902, Organes agglutinantes et organes cilio-phagocytaires, ibid. (3), Vol. 10.

13. Diesing, K., 1859, Revision der Myzhelminthen. Abtheilung Bdelliden, in: SB. Akad. Wiss. Wien, math.-nat. Cl., Vol. 33.

14. Graf, A., 1894, Beiträge zur Kenntniss der Excretionsorgane von Nephelis vulgaris, in: Jena. Z. Naturw., Vol. 28.

15. —, 1899, Hirudineenstudien, in: Nov. Act. Acad. Leop. Carol., Vol. 72.

16. Grube, E., 1851, Annulaten, in: Dr. A. Th. v. Middendorff's sibirische Reise, Vol. 2, T. 1.

17. Hesse, R., 1894, Zur vergleichenden Anatomie der Oligochaeten, in: Z. wiss. Zool., Vol. 58.

18. —, 1896, Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. I. Die Organe der Lichtempfindung bei den Lumbriciden, ibid., Vol. 61.

19. Kessler, K., 1868, Материалы для познанія Онежскаго озера и Обонежскаго края, преимущественно въ зоологическомъ отношеніи, in: Приложеніе къ трудамъ перваго съѣзда русскихъ естествоиспытателей, СПб.

Kowalevsky, A., 1896, Étude sur l'anatomie de l'Acanthobdella peledina, in: Bull. Acad. Sc. St. Pétersbourg, Vol. 5, No. 4.

—, 1897, Études biologiques sur les Clepsines, in: Mém. Acad. Sc. St. Pétersbourg, Cl. phys.-math. (7), Vol. 5, No. 3.

—, 1900, Étude biologique de l'Haementeria costata Müller, ibid., Cl. phys.-math. (7), Vol. 11, No. 1.

20. Lang, A., 1894, Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere, Jena.

21. —, 1903, Beiträge zu einer Trophocöltheorie, in: Jena. Z. Naturw., Vol. 38.

22. Leuckart, R., 1894, Die Parasiten des Menschen, 2. Aufl., Vol. 1, Lief. 5, Leipzig.

23. • Leydig, F., 1864, 1. Vom Bau des thierischen Körpers, Tübingen.

—, 1864, 2. Tafeln zur vergleichenden Anatomie, Tübingen.

24. Livanow, N., 1902, Die Hirudineen-Gattung Hemiclepsis Vejd., in: Zool. Jahrb., Vol. 17, Syst.

25. —, 1903, Untersuchungen zur Morphologie der Hirudineen. I. Das Neuro- und Myosomit der Hirudineen, ibid., Vol. 19, Anat.

26. —, 1904, 1. Die Darmmuskulatur der Oligochaeten und Hirudineen, in: Zool. Anz., Vol. 27, No. 19.

27. —, 1904, 2. Untersuchungen zur Morphologie der Hirudineen, II. Das Nervensystem des vorderen Körperendes und seine Metamerie, in: Zool. Jahrb., Vol. 20, Anat.

28. McKim, D., 1895, Ueber den nephridialen Trichterapparat von Hirudo, in: Z. wiss. Zool., Vol. 59.

Moore, J. P., 1895*, The anatomy of Bdellodrilus illuminatus, an American Discodrilid, in: Journ. Morphol., Vol. 10.

—, 1900, A description of Microbdella biannulata with especial regard to the constitution of leech somite, in: Proc. Acad. nat. Sc. Philadelphia, Vol. 6.

29. Mrázek, Al., and F. Vejdovsky, 1902, Ueber Potamothrix (Clitellio?) moldaviensis n. g. n. sp., in: SB. böhm. Ges. Wiss., Prag.

30. Oka, A., 1894, Beiträge zur Anatomie der Clepsine, in: Z. wiss. Zool., Vol. 58.

31. —, 1902, Ueber das Blutgefäßsystem der Hirudineen, in: Annotat. zool. Japon., Vol. 4, p. 2.

Perrier, Éd., 1897, Traité de Zoologie, Fasc. 4, Paris.

32. Poppius, B., 1900*, Förekomsten af Acanthobdella i våra lappmarker, in: Meddel. Soc. Fauna Flora fenn., Vol. 24.

33. Retzius, G., 1891, Zur Kenntniss des centralen Nervensystems der Hirudineen, in: Biol. Unters. (N. F.), Vol. 2.

Rich, W., 1902, Studies in Earthworm chloragogue, in: Biol. Bull., Vol. 3.

34. Schmidt, F., 1903, Die Muskulatur von Branchiobdella parasita, in: Z. wiss. Zool., Vol. 75.

35. Schneider, G., 1896, Ueber phagocytäre Organe und Chloragogenzellen der Oligochaeten, ibid., Vol. 61.

36. Schultze, O., 1883, Beiträge zur Anatomie des Excretionsapparats (Schleifencanale) der Hirudineen, in: Arch. mikrosk. Anat., Vol. 22.

37. Semper, C., 1876, Die Verwandtschaftsbeziehungen der gegliederten Tiere, III. Strobilation und Segmentation, in: Arb. zool.-zoot. Inst. Würzburg, Vol. 3.

38. Vejdovský, F., 1883, Exkreční soustava Hirudinei, in: Kral. české společnosti nauk.

39. —, 1884, System und Morphologie der Oligochaeten, Prag.

40. — und Al. Mrázek, 1902, Ueber Potamothrix (Clitellio?) moldaviensis n. g. n. sp., in: SB. böhm. Ges. Wiss., Prag.

Whitman, C., 1892, The metamerism of Clepsine, in: Festschr. Leuckart, Leipzig.

Translation of non-French and non-English titles in the literature

1. Analysis of the external body structure of Hirudinea.
2. The leading element of the nervous system and its topographic relationships to the cells.
3. The three different forms of photoreceptor cells in Hirudinea.
4. Hypodermis and new sensory organs in the skin of Rhynchobdellids.
5. The metamorphosis of *Aulastoma gula*
6. On the metamorphosis of *Nephelis*
7. Preliminary study on the function of chloragogen cells in the genera *Lumbricus* and *Allolobophora*
8. The parasites of man.
9. Contributions to the ontogenesis of the Hirudinea. On the embryology of *Nephelis*
10. New contributions to the ontogenesis of the Hirudinea. On the embryology of *Hirudo medicinalis* and *Aulastomum gula*
11. On the excretory organs, the coelom and the blood vessels of the Hirudinea.
12. Further contributions to the ontogenesis of the Hirudinea. On the embryology of *Clepsine*
13. Revision of the Myzhelminthes. Family of Bdellidae.
14. Contributions to the study of the excretory organs of *Nephelis vulgaris*
15. Hirudinean studies.
16. Annulata.
17. On the comparative anatomy of Oligochaeta.
18. Studies on the photoreceptor organs in the lower animals.

19. Kessler, K. Contribution to the knowledge of Lake Onega and surrounding area, particularly in regard to zoological data. In: Appendix to the reports read at the First Congress of Russian Naturalists. St. Petersburg, 1868.

20. Textbook of comparative invertebrate anatomy.

21. Contribution to a trophocoel theory.

22. The parasites of man.

23. On the body structure of animals.

24. The Hirudinean genus *Hemiclepsis* VEJD.

25. Studies on the morphology of the Hirudinea.

26. The intestinal musculature of Oligochaeta and Hirudinea.

27. Studies on the morphology of the Hirudinea.

28. On the nephridial funnel apparatus of *Hirudo*.

29. On *Potamothrix* (*Clitellio*?) *moldaviensis*.

30. Contributions to the anatomy of *Clepsine*.

31. On the blood vessel system of the Hirudinea.

32. Occurrences of *Acanthobdella* in our Lappish territories.

33. On the knowledge of the central nervous system of the Hirudinea.

34. The musculature of *Branchiobdella parasita*.

35. On phagocytic organs and chloragogen cells in Oligochaeta.

36. Contributions to the anatomy of the excretory apparatus (nephridial canals) of the Hirudinea.

37. The relationships of annulates. III. Strobilation and segmentation.

38. The excretory system of the Hirudinea.

39. System and morphology of the Oligochaeta.

40. On *Potamothrix* (*Clitellio*?) *moldaviensis* n.g.n.sp.

Explanation of illustrations

Figures 33 - 41

In the colour illustrations, the skin epithelium and its invaginations, as well as the giant gland cells of the inner body mesenchyme and the chaetae are drawn in dark grey, the mesenchyme in light grey, the nephridia in dark green, the nervous system and the sensory organs in yellow, the coelom and the male reproductive apparatus in orange-yellow, the female reproductive system in orange-red, the blood vessel system in red, and the intestine in blue. The somites are numbered from 1 to 29, and their annuli from I to IV. Qs = cross section of the body, Fs = frontal section of the body, Sts = sagittal section of the body.

General abbreviations

adz	albumin gland cell
agn	anal ganglion mass
ah	posterior cavity of the female reproductive apparatus
am	amoebocytes of the mesenchyme
an	endgut
ap	accessory follicles of ganglion cells
au	(au_1, au_2, au_3) eye (of the 1st, 2nd, 3rd pair)
aup	secretory duct clusters of the giant gland cells of the mesenchyme
bs	(bs_{1-5}) chaetae (of the 1st - 5th head somite)
bsz	cells of the chaetal sacs
bz	blood cells
c	coelom and its sectors

cd	coelom gland
cdz	cells of the coelom gland
cfm	central fibre mass of the ganglia
clz	chloragogen cells
cn	connective and connective trunks
cs	coelom outpouchings
ct	coelothelium and its cells
cu	cuticle
cy	cytophore
cz	coelomocytes
d	midgut
de	ejaculatory duct
dep	intestinal epithelium
dg	dorsal blood vessel
dm	diagonal musculature and its cells
dmt	dorsomedian part of the nephridium
dn	dorsal branch of the posterior nerve of the somite
dph	pharyngeal sector provided with secretory ducts
ds	blood sinus of the hindgut
dsp	dissepiment
dsz	dissepiment muscle cells
dvm	dorsoventral muscles
dz	gland cells of the epithelium
ep	skin epithelium and its cells
gdz	giant gland cells of the mesenchyme
gep	large skin epithelium cells
gh	blood vessel cavity

gl	marginal lamella of the mesenchyme
gn	ganglion of the ventral cord
gnz	ganglion cells
gz	glia cells
h	testis and its spermatogenetic zone
hd	hindgut
hnz	branch of the posterior ring nerve of the somite leading into the 4th somite annulus
hs	attachment disk
int	intermediate line of the body, its muscle strands and sensory organs
is	inner cell layer (in various organs)
l	lateral line of the body
lb	lateral longitudinal muscle strand
lm	longitudinal musculature and its cells
ln	lateral nerve
lp	lateral ganglion cell follicles
m	buccal opening
md	median line of the body
mf	muscle fibre
mh	buccal cavity
ml	mesenchyme lamella of the esophagus
mn	median nerve
mp	median ganglion cell follicles
ms	mesenchyme
mz	muscle cell
n	nerve
nph	(nph_6 - nph_{19}) nephridia (of the 6th - 19th somite)

npz	nephridial cells
nrz	nutritive cells of the reproductive apparatus
nz	nerve cells of the large nerve tubes
obm	supraesophageal ganglion mass
oc	ovocytes
oe	esophagus
oep	epithelium of the esophagus
olm	muscle cell of Oligochaete type
ov	ovisac
ovp	epithelium of the ovisac
phf	pharyngeal fold
pmd	paramedian line of the body, its muscle strands and sensory organs
pmv	paramarginal line of the body, its muscle strands and sensory organs
pr	protractors of the esophagus
pz	pigment fat cells
qg	lateral blood vessel
rg	ring-shaped blood vessel
rm	circular musculature and its cells
rmf	circular muscle fibre of the anterior ring nerve of the somite
rn	(rn_1, rn_2) anterior and posterior ring nerve of the somite
rz	retinal cell ("subepidermal" cell)
scn	pharyngeal connective
sgn	stomodeal ganglion
sk	sensory papilla
sm	diagonal muscles
sn	sensory nerve (of the somite)
spt	spermatheca

st	sperm funnel of the male reproductive apparatus
sz	spermatocytes
vd	sperm duct
vg	ventral blood vessel
ut	discharge duct of the female reproductive apparatus

Fig. 33

No. 1. Schematic representation of the body structure of *Acanthobdella*, showing the distribution of somites and their annulation, the chaetae (bs_1-bs_5), the eyes (au_1 - au_3), the nervous system (obm, gn, cn), the intestine (oe, d, hd), and the nephridia (nph_{6-19}) as well as the male (h, ø) and female (ov, ah, spt, ↓) reproductive organs. Dotted lines show the somite boundaries (1-29) on one side and the boundaries of the body regions on the other side.

No. 2. Half schematic cross section of the mid sector of the 3rd somite (3) of the head region. The ventral body surface is flattened and greatly shortened. Its longitudinal muscle strands are formed only by the paramedian (pmd_1), intermediate (int_1) and paramarginal (pmr_1) muscle bundle. The muscle fibre of Oligochaete type, running dorsally, is already lacking here. Laterally we find a part of the chaetal sac (bsz_3) of the lateral pair of the 3rd head somite, laterad of the same lies the corresponding diagonal muscle cell and mediad lies a diagonal cell that belongs to the ventral pair of chaetae of the 3rd head somite (not visible in the section). Further mediad is found a part of the chaetal sac (bsz_2) of the lateral pair of the 2nd head somite with the associated diagonal muscle cell; this part protrudes far into the coelom (c). In the coelom between this muscle cell and that of the ventral pair of chaetae of the 3rd somite is a cell (pr_3) of the middle pair of protractors of the esophagus. Dorsally within the mesenchyme (ms) near the median line of the body are 2 cells ($pr_{1,2}$) of its anterior protractors. Medially in the coelom a part of the chaetal sac (bsz_1) of the ventral pair of the 1st head somite can be seen. Between it and the esophagus (oe) the supraesophageal ganglion mass (obm) protrudes into the coelom below which a dorsoventral muscle cell (dvm_2) of the median pair of the 2nd somite is situated. Dorsally in the inner body mesenchyme are 3 follicles originating in the dorsal group of secretory ducts of the giant gland cells , and ventrally 3 follicles (aup) of the ventral group are embedded. The coelom (c) is greatly restricted by the organs lying within it. The ventral blood vessel (vg) has just divided into its 2 terminal branches, and the dorsal blood vessel is seen before it has divided. Its mesentery is well-developed in the dorsal part. Slightly laterad of it in the inner body mesenchyme is the lateral vessel (qg) of the 2nd pair whose descending sector in visible in the coelom at the chaetal sac. The esophagus (oe) dorsally contains 2 still distinguishable secretory ducts of the giant gland cells, and visible against it is the mesenchyme lamella (ml) with a muscle cell. This lamella unites with the esophageal wall on the lateral line of the esophagus. The ventral bundles of secretory ducts represent a mass. The section is slightly diagonal, so that ventrally a sector is seen that lies slightly anterior of the dorsal sector; this is caused by the position of the body somites in relation to each other[1]. Scale: 150:1.

No. 3. Half schematic cross section of the 2nd annulus of the 5th somite of the head region (5). The ventral body surface is flattened and shorter than the dorsal surface; for that reason the ventral (bs) and the lateral (bs*) pair of chaetae are facing ventrad. The longitudinal muscle strands (pmd$_1$, int$_1$, pmr$_1$) are ventrally much condensed. The sensory organs (sk) on the ventral side protrude into the inner body mesenchyme. The eye (au$_3$) is drawn with a dotted line, since it is situated slightly cephalad of the section illustrated, but the chaetae are drawn with solid lines, although only parts of these are included in the section. Dorsally of the lateral group of sensory papillae lies a small accessory papilla (sk*). In the inner body mesenchyme (ms) groups of follicles of secretory ducts (aup) of the giant gland cells are embedded whose cell bodies are not shown in the illustration. The lateral group divides into 3 follicles, the dorsal and ventral groups each give off one follicle which extends to the esophagus. The coelom (c) laterally reaches almost to the lateral longitudinal muscle strands. Ventrally they contain the ventral ganglion (gn) of the 5th head somite and the ventral blood vessel (vg), both of which are quite free. The dorsal blood vessel (dg) occupies the dorsal sector of its mesentery. The esophagus also contains the circular muscle fibres. Scale: 1:150.

---

[1] In this and all other schematic views, the mesenchyme cells are not shown to avoid congestion of the drawings.

No. 4. Half schematic cross section through the 1st preclitellar somite (6) at the boundary between its 1st and 2nd annulus. A considerable shortening of the ventral somite surface can be observed. On the ventral intermediate line (int$_1$) lies the excretory nephridial sector (nph$_6$*) of the 1st preclitellar somite. The two legs of its excretory sector (nph$_6$) lie on both sides of the coelom outpouching (cs$_7$) of the 2nd preclitellar somite. In addition the inner body mesenchyme contains giant gland cells (gdz) and their secretory duct clusters (aup). Visible in the well-developed coelom sinus (c) of the 1st preclitellar somite are the connective (cn) of the ventral cord, the ventral blood vessel (vg) with the posterior pair of lateral vessels (qg), the esophagus (oe) anterior of the transition into the midgut, and the dorsal blood vessel (dg) of whose mesentery only the dorsal sector remains. Scale: 100:1.

No. 5. Half schematic cross section through the middle sector of the 3rd preclitellar somite (8). The inner body mesenchyme (ms) of the typically developed body wall (cp, rm, dm, lm) contains dorsoventral (dvm) and diagonal (sm) muscles and the giant gland cells (gdz) with their secretory duct clusters (aup). The well-developed coelom (c) forms the lateral outpouching here. Freely situated in it are the connective (cn) of the ventral cord, the ventral blood vessel (vg) and the midgut with its chloragogen layer (clz). The dorsal blood vessel (dg) is connected with the intestinal wall by means of the ventral sector of the mesentery. Scale: 100:1.

No. 6. Half schematic cross section through the 1st clitellar somite (9) at the boundary of its 1st and 2nd annulus. In the typically formed body wall the diagonal muscle cell (dm*) can be seen. In the inner body mesenchyme are a diagonal muscle cell (sm), the giant gland cells and their secretory duct clusters. The wall of the testis (h) almost touches the coelom sector which surrounds the intestine and which is completely filled with coelothelium elements (ct*). A sort of segregated dorsal coelom sinus (c) is present here which contains the dorsal blood vessel (dg). Of the mesentery of the latter only the ventral sector remains. The anterior coelom sector (c_1) forms a true ventral coelom sinus that is separated from the remaining coelom space by a mesenchyme lamella. In this coelom sinus the ventral blood vessel (vg) and the connective of the ventral cord (cn) are freely contained. Scale: 100:1.

Fig. 34

No. 7. Half schematic cross section through the dissepiment between the 2nd (7) and 3rd (8) preclitellar somite. The typically formed body wall with the giant gland cells and their secretory duct clusters in the inner mesenchyme. Protruding into the coelom outpouching (cs_1) of the 3rd preclitellar somite, which is situated laterally of the intestine in the mesenchyme, is the caudal part of the excretory nephridial sector (nph_7) of the 2nd preclitellar somite. From the upper quadrant of the esophagus extend 2 dissepiment muscle cells (dsz), from the lower quadrant extends one such cell (dsz_1). Dorsally and ventrally the dissepiment has one opening each, through which the coelom of the 2 adjacent somites communicates. The ventral opening (c_1) freely contains the ventral blood vessel and the connective of the ventral cord, the dorsal opening (c) contains the dorsal blood vessel which retains the ventral sector of its mesentery. The latter is traversed by the fibres of a dissepiment muscle cell (dsz). Scale: 75:1.

No. 8. Half schematic cross section through the 2nd annulus of the 2nd clitellar somite (10). In the typically formed body wall is the sensory nerve (sn) of the somite which ends just before the dorsal median line of the body; it carries a small ganglion (gnz) on the ventral intermediate line and another on the lateral line. The groups of sensory papillae (sk) it innervates are dorsally and ventrally arranged along the paramedian (pmd, pmd_1), intermediate (int, int_1) and lateral lines of the body. In the inner mesenchyme, 2 giant gland cells are adjacent to the testes (h). The ventral coelom sector (c_1) is separated from the remaining coelom cavity (c) surrounding the intestine and forms a true ventral coelom sinus in which are the free connective of the ventral cord and the ventral blood vessel. The latter still has the dorsal sector of its mesentery. All around the intestine, the coelom (c) forms a narrow cavity that only widens dorsally, where the dorsal blood vessel lies in it quite freely. The intestine is covered by the layer of chloragogen cells (clz). Scale: 75:1.

No. 9. Half schematic cross section at the boundary between the 2nd (10) and 3rd (11) clitellar somite. At the ventral median line of the body, the typically formed body wall has an indentation of the skin epithelium representing the spermatheca (spt). 2 muscle cells (dsz_1) extending near the two inner muscle cells (mz) of the basal ovisac sector extend toward the latter from the lower quadrant of the intestine. Laterally to these 2 muscle cells the coelom gland (dc) is seen whose ventral part protrudes into the posterior cavity (ah) of the female reproductive apparatus, while the dorsal part, which enters the coelom (c) of the 3rd clitellar somite (11), forms the basal sector of the ovisac. The inner body mesenchyme, in which the outer muscle cell of the basal ovisac sector is embedded, enters between these two parts of the coelom gland. The posterior cavity of the female reproductive apparatus consists of outpouchings which enter between the ventral longitudinal muscle bundles. In the inner body mesenchyme are the testis (h) and 3 giant gland cells as well as the dorsal, very thick dissepiment muscle cells (dsz). The ventral blood vessel and the connective of the ventral cord extend quite freely inside a narrow coelom sinus (c_1). All around the dorsal blood vessel (dg), which has a muscular sphincter in this place, the coelom is absent completely. Scale: 75:1.

No. 10. Half schematic cross section through the 3rd annulus of a somite of the midgut region. In the typically formed body wall lies the posterior ring nerve of the somite (rn_2) which communicates with the paramedian (pmd, pmd_1), intermediate (int, int_1) and paramarginal (pmr, pmr_1) longitudinal muscle strands of the dorsal and ventral side as well as with the lateral (lb) longitudinal muscle strand. The said nerve carries 3 bipolar nerve cells (nz) of the large tubes and a small lateral ganglion (gnz). In the inner body mesenchyme are the voluminous testis (h), a diagonal muscle cell (sm), and 3 giant gland cells. The coelom is slightly widened ventrally and dorsally; it forms an inconspicuous lateral outpouching (c*). In it lies the voluminous midgut surrounded by the chloragogen cell layer (clz); below the midgut are the connective of the ventral cord and the ventral blood vessel; above the midgut are the dorsal blood vessel and the ovisacs (ov). Scale: 75:1.

No. 11. Half schematic cross section in the region of one of the most posterior dissepiments of the mid body. The inner mesenchyme of the typically formed body wall contains the testis and the giant gland cells. A pair of dorsal (dsz) and a pair of ventral (dsz_1) dissepiment muscle cells as well as 2 dorsoventral muscle fibres (dvm) can be seen. The dorsal opening (c) of the dissepiment is well-developed. Here the coelom contains the ovisacs (ov) and the dorsal blood vessel. In the coelom sinus of the ventral dissepiment opening (c_1) are the connective of the ventral cord and the ventral blood vessel which is suspended by a mesenchyme strand that contains the process of a fairly small dissepiment muscle cell (dsz_1). The intestine is restricted and forms rather conspicuous folds. Scale: 75:1.

No. 12. Half schematic cross section at the boundary between the 1st and 2nd annuli of the 1st somite of the hindgut region (20). In the typically formed body wall a diagonal muscle cell (dm*) is seen; embedded in the inner mesenchyme are a few giant gland cells whose secretory duct clusters are very evenly distributed here. The coelom (c) surrounds the hindgut in the form of a narrow slit that slightly widens ventrally (c_1) where it contains the ventral blood vessel and the ganglion (gn) of the ventral cord. Toward the coelom in the wall of the hindgut are longitudinal muscle fibres

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINEE A LA PUBLICATION

(lm) followed by 2 lamellae of the mesenchyme layer of the intestinal blood sinus (ds). The latter openly communicates with the dorsal blood vessel (dg) which extends dorsally in the coelom. Scale: 75:1.

Fig. 13. Half schematic cross section through the last dissepiment of the body which externally corresponds to the boundary between the 4th (23) and 5th (24) somite of the hindgut region. The body wall has the usual structure, but a few muscle fibres have shifted quite far into the inner body mesenchyme. The mesenchyme contains quite a few small secretory duct clusters of the giant gland cells which are not shown in the illustration. The coelom (c) only forms a small ventral opening in the dissepiment; characteristic for the latter are 2 ventral dissepiment muscle cells (dsz_1). Quite free in the coelom are the ganglion of the ventral cord and the ventral blood vessel in whose mesenchyme layer the secretory duct of a giant gland cell is embedded. The hindgut (hd) and endgut (an) are seen; the latter opens externally here. Below the intestinal epithelium in the mesenchyme is one of the two blood vessels resulting from the division of the dorsal vessel in the area of the 6th somite (25) of the hindgut region. Beginning at the transition between hindgut and endgut, circular and longitudinal muscles are situated below the epithelium of the endgut. Scale: 75:1.

No. 14. Half schematic cross section at the boundary between the hindgut and attachment disk region. The ventral half of the body. Below the skin epithelium lies the circular muscle layer, while the diagonal musculature is absent; the longitudinal muscles extend through the entire width of the mesenchyme and form very thick strands. In the interspaces between the latter are the lateral blood vessels (qg) which extend along the paramedian (pmd_1), intermediate (int_1) and lateral (l) lines of the body. The giant gland cells and their secretory ducts are not shown in the illustration. In the centre is the coelom sac (c). Scale: 75:1.

Fig. 35

No. 15. Half schematic cross section through the attachment disk region just before the ring-shaped blood vessel. The ventral body half. Below the skin epithelium (ep) are the circular muscle fibres (rm). The inner mesenchyme is filled throughout with the longitudinal muscle bundles (lm). Peripherally between them the lateral blood vessels (qg) are seen on the paramedian (pmd_1), intermediate (int_1) and lateral (l) lines of the body. Scale: 100:1.

No. 16. Half schematic cross section through the 5th (24) and 6th (25) somites of the hindgut region. The concavity of the attachment disk is very distinct. At the margin of the attachment disk a longitudinal muscle fibre (lm*) is seen to perforate the circular muscle layer (rm). The circular muscle fibres are evenly distributed over the entire concavity of the disk, and only in the middle of the disk is a separate circular muscle bundle (rm*). The longitudinal muscle strand (lm) spreads in fan-like fashion toward the centre. On the concavity of the disk the longitudinal muscles extend peripherad from the circular muscles. On the margin of the disk a muscle fibre (mf) is seen that extends radially. Between it and the longitudinal muscles lies the ring-shaped blood vessel (rg). One of the lateral nerves (n_3) of the anal ganglion mass enters the mesenchyme of the attachment disk from the posterior sac-like coelom sector (c). Scale 100:1.

No. 17. Half schematic view of the head region. Left: the dorsal body surface under which the ventral side has been projected. The arrangement of the eyes (au_{1-3}) is also shown. Right: the ventral body surface on which the position of the chaetal sac openings (bs_{1-5}) has been plotted. The somite boundaries (1-5) are drawn as dotted lines. Scale 100:1.

Fig. 18. Schematic representation showing the arrangement of dissepimental, dorsoventral and diagonal muscles of the head region. The small cells (dsz_{1-5}) coming from the esophaogus (oe) represent the ventral dissepiment muscles of the head somites (1-5). Their dorsal muscles form protractors (pr_{1-4}) of the esophagus. The row of lateral ovals represents the cross sections of the diagonal muscle cells (sm) of the head somites, while the ovals closer to the median line are the cross sections of the dorsoventral muscles (dvm_{1-5}). The diagonal musculature is shown in the plane of the lateral lines of the body; only the ventral part of the dorsoventral musculature is shown.

No. 19. Schematic view of the ventral pair of chaetae of the 5th head somite (5). Because it is seen from the side of the lateral line of the body, only one chaeta (bs_5) is visible. The diagonal muscle cell of the chaetal apparatus is not shown, since it would almost completely obscure the chaeta. 2 cells (mz_2) of the muscle apparatus extend caudad and toward the lateral line of the body; one (mz_1) 1 extends caudad and toward the ventral intermediate line, 4 attach themselves to the integument near the chaetal sac opening, and 1 muscle cell (mz) extends cephalad toward the ventral intermediate line. The inner chaetal end protruding into the coelom sinus is covered with a coelothelial coating (ct). Scale: 150:1.

No. 20. Schematic representation of the circular musculature of a somite annulus. Shown is one (the ventral or dorsal) side of the body flattened out over the entire circumference of a somite annulus. Along the anterior and posterior margins of the annulus are fairly conspicuous circular muscle bundles (mf); in the middle sector of the annulus, 2 types of muscle bundles (a, b) occur. The position of their nucleate cell sectors is indicated for all muscle fibres.

No. 21. Schematic representation of the diagonal musculature of a somite. The ventral body side is shown flattened out along a distance covering about 1 1/2 somites. On the lateral line of the body is the nucleate sector (dm*) of the diagonal muscle cell. The fibres of 2 such cells form the entire diagonal musculature of a given somite. Extending ventrad and caudad, the diagonal muscle fibres change their respective position on the median line (md). Some muscle fibres are given off by the dorsal protoplasmic process of the muscle cell.

No. 22. Schematic representation of the longitudinal musculature of a mid body somite. The left vertical row (a) contains the ventral longitudinal fibres from the median line (top) to the paramarginal longitudinal strand (pmr_1, bottom). The right row (b) represents the dorsal muscle fibres from the median line (top) to the lateral longitudinal muscle bundle (bottom). The distribution into separate muscle bands is marked by larger spaces between 2 adjacent muscle fibres. The paramedian (pmd_1, pmd), intermediate (int_1, int), paramarginal (pmr_1, pmr) and lateral (lb) muscle strands can be seen. The type of the individual muscle cells can be recognized from the representation of their nucleate sectors. There are muscle cells of Hirudinean type (mz), cells (mz*) in which the contractile-fibrillar layer is incomplete over a certain length of the periphery, and cells of Oligochaete type (olm).

Fig. 36

No. 23. Cross-section of the skin epithelium. Between some ordinary epithelial cells (ep) are 2 particularly "large" cells (gep). From one side (the outside) can be seen a well-formed cuticular lamella (cu), from the other side (the inside) the straight contour of the mesenchymatous marginal lamella (gl). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 24. Cross-section. 3 cells of the skin epithelium (ep); extending between them as far as the cuticle are processes (mf) of the circular muscle fibre of the anterior ring nerve of the somite. The contour of the basal epithelial surface looks irregularly wavy. Hermann's fluid, iron hemotoxylin. Scale: 800:1.

No. 25. Cross-section. Ordinary skin epithelium (ep) with irregular basal contour: in one cell a mitosis is visible. From the epithelium 2 sensory papillae (sk) of the lateral line of the body protrude into the mesenchyme. The dorsally situated papilla contains only ordinary sensory cells; in the middle papilla a well-developed subepithelial (retina) cell (rz) with its light-refracting inner body can be seen lying proximally between the ordinary sensory elements. Of the 3rd ventral sensory papilla, only a single sensory cell is visible in the mesenchyme. The proximal ends of the said sensory papillae continue in the nerve cluster of the sensory nerve. Between the two dorsal papillae is a part of the diagonal muscle fibre (dm). Hermann's fluid, iron hemotoxylin. Scale: 450:1.

No. 26. Cross-section. The body wall near the lateral line. The skin epithelium (ep) is sectioned diagonally, since the following sections show the annular furrow; it therefore looks as if it had several layers. An circular muscle cell with a pear-shaped nucleate sector (rm), diagonal (dm) and longitudinal (lm) muscle fibres. One of the latter (lm*) is without the contractile-fibrillar layer over a short distance, where the nucleate cell sector begins. Inside the mesenchyme lies a pigment fat cell (pz), followed by the coelothelial membrane (ct) of the testis. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 27. Cross-section. The body wall of the lateral line. The typically developed skin epithelium (ep) contains some gland cells (dz) in various functional phases. The nucleate sector of an ordinary circular muscle fibre (rm) in which the lateral nerve (ln, stained almost black) is impressed; distad of this muscle cell are 2 mesenchyme cells whose nuclei are not visible in the section. Diagonal (dm) and longitudinal (lm) musculature. One of the longitudinal muscles (lm_1) has the nucleus in the centre and is entirely of Hirudinean type. In the mesenchyme is a group of 3 small pigment fat cells (pz) and one such cell of very substantial size; also visible are 2 amoebocytes (am). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 28. Cross-section. The body wall. Typically developed skin epithelium (ep). Below it is a circular muscle cell (rm) that seems to be of Hirudinean type; however, the following sections clearly show the slit in the contractile-fibrillar layer. Diagonal (dm) and longitudinal (lm) muscles. The latter, except one fibre (left), form the dorsal paramarginal longitudinal muscle strand in which one of the two muscle fibres closely comunicating with the ring nerves (lm*) is seen at the beginning of its nucleate sector; the same sector is visible of the Oligochaete muscle fibre (olm). In the mesenchyme can be seen an amoebocyte, 2 pigment fat cells and one albumin gland cell (adz) which is ceasing to function. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 29. Sagittal section. The body wall at the boundary of the 1st and 2nd somite annuli. Below the skin epithelium (ep) lies the circular muscle layer (rm) with 3 nucleate cell sectors (bottom). The lateral nerve (ln) and the diagonal muscle cell (dm*) with its muscle fibres (dm) are visible; the protoplasmic process extending dorsad is visible in the beginning sector. The diagonal muscle fibres originating from the respective cell of the other side come to lie more toward the outside. Longitudinal muscle bundles (lm) and pigment fat cells (pz). Sublimate acetic acid, hemalum. Scale: 150:1.

No. 30. Cross-section. The body wall in the annular furrow between the 1st and 2nd annulus of a somite. A circular muscle fibre (rm) with lateral nerves (ln) impressed into the latter and the skin epithelium (ep); the nucleate sector (dm*) of a diagonal muscle cell and its muscle fibres (dm); longitudinal muscles (lm), a pigment fat cell (pz), and free amoebocytes (am). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 31. Cross-section. Paramedian longitudinal muscle strand of the dorsal side. Hermann's fluid, iron hematoxylin. Scale: 550:1.

No. 32a. Cross-section. 2 greatly ramified dorsoventral muscle cells (mz) of the dissepiment between the 1st (20) and 2nd (21) somite of the hindgut region. The contractile-fibrillar layer traverses the nucleate sector in the form of separate fibres. The fine filaments (gl) at the periphery of the muscle cells are branches of the mesenchymatous marginal lamella. b. The following section. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 300:1.

No. 33. Cross-section. A pigment fat cell (pz) with inclusions of the fat-like substance and with a finely pigmented seam. Hermann's fluid, unstained. Scale 300:1.

No. 34. Cross-section. A part of the body mesenchyme with 2 longitudinal muscles (dm); 3 pigment fat cells (pz) with 2 albumin gland cells (adz). Sublimate acetic acid, hemalum. Scale: 400:1.

No. 35. Cross-section. Giant gland cells (gdz) of the inner body mesenchyme of the 1st preclitellar somite (6); the laterally sectioned secretory duct clusters (aup) of the same. Right: phases of the progressive development and growth of these cells (gdz_{1-3}), in the middle are 2 gland cells (gdz_{4-5}) of maximum size, left: stages of of their regressive change (gdz_{6-7}). 2 amoebocytes of the mesenchyme (am). Sublimate acetic acid, hemalum. Scale: 300:1.

No. 36. Cross-section. The wall of the midgut in the 3rd preclitellar somite (8). Low intestinal epithelium (dep), thin mesenchyme layer (ms) with laterally sectioned longitudinal fibres (lm), typical chloragogen cells (clz), one of which includes a mitotic division figure; in the coelom a free coelomocyte (cz). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 37. Frontal section. The wall of the midgut in a somite of the midgut region. Typical intestinal epithelium (dep) with inconspicuous folds. Mesenchyme layer (ms) and distad of its marginal lamella the chloragogen cell layer (clz); circular muscle cells (rmz) traverse the basal sectors of the cells of the latter; in the middle of this section, the said layer contains a typical coelothelial muscle cell (cmz) and 2 of the lamellae of a contractile-fibrillar substance (abbreviation illegible) originating there; these are followed by the coelom (c) with a free coelomocyte (abbreviation illegible). Sublimate acetic acid, hemalum, Scale: 450:1.

Fig. 37

No. 38. Cross-section. The intestinal wall and the coelom (c) in a mid body somite. Typical epithelium (dep) of the midgut. Mesenchyme layer (ms) with longitudinal muscle fibres (lm); the nucleate sector (lm*) of one longitudinal fibre can be seen. Along the outer marginal lamella of the mesenchyme is an circular muscle fibre (rm) whose coelothelial muscle cell (rm*) lies between the ordinary chloragogen cells (clz). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 39. Frontal section. Intestinal wall and dissepiment in the mid body. The typical epithelium of the midgut (dep) forms a pronounced ring-shaped fold at the somite boundary below which 2 circular muscle fibres (rm*) are embedded in the mesenchyme layer (ms). Distally of the outer marginal lamella of the mesenchyme lies the chloragogen cell layer (clz) with circular muscle fibres (rm) at its basal cell sectors. The intestinal mesenchyme (ms) directly merges with the mesenchyme (ms*) of the dissepiment, where 3 dorsoventral muscle cells (dvm) are embedded. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 550:1.

No. 40. Frontal section. Wall of the midgut with typical epithelium (dep) forming folds at the somite boundary; inside the mesenchyme layer (ms) is a longitudinal muscle fibre (lm), and below the epithelial fold are 2 circular muscle fibres (rm*). The other circular muscle fibres (rm) lie distally of the outer marginal lamella of the mesenchyme at the basal sectors of the typical chloragogen cells (clz); adjacent to the latter a free coelomocyte is situated in the coelom. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 550:1.

No. 41. Cross-section. An ordinary ganglion of the ventral cord lying in the coelom, covered with somatic coelothelium (cl); a cell (cl*) of the latter is visible laterally. The central fibre mass (cfm) of the ganglion contains a median glia cell (gz); into this mass protrude the cell processes of the two lateral (lp) and of one median (mp) ganglion cell follicles. In each lateral follicle 1 glia cell (gz) with an apparently vacuolized protoplasm is visible. The neurilemma sheath of the ganglion directly merges with the inner body mesenchyme (ms); dorsally it contains longitudinal muscle fibres (mf). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 42. Cross-sectional view. Ganglion of the ventral cord in a clitellar somite, sectioned slightly obliquely from right to left. The ganglion is almost completely depressed into the inner body mesenchyme (ms) and contains 2 lateral (lp) and 1 median (mp) ganglion cell follicles; also visible are the accessory follicles (ap) of ganglion cells directly entering the central fibre mass (cfm). Dorsally in the neurilemma are the longitudinal muscle cells (mf). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 43. Cross-sectional view. Connective of the ventral cord. The median nerve bundle is united with one of the two connective trunks (cn), the other contains a connective cell (gz). In the neurilemma (ms) are longitudinal muscle fibres (mf). The coelothelial coating (ct) contains a typical somatopleural xell (ct*). Sublimate acetic acid, hemalum. Scale: 800:1.

No. 44. Cross section through a longitudinal muscle fibre with typical motoric nerve ending. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 45a, b, c, d. Cross-section. 4 successive sections. The posterior ring nerve (rn_2) of the somite is traversed by the dorsal paramedian longitudinal muscle strand (lm). This causes the formation of deep grooves on the longitudinal muscle fibres. Also visible are 3 diagonal muscle fibres (dm) and 2 mesenchyme cells (am). A longitudinal muscle cell (lm_1) of pronounced Hirudinean type; the nucleate cell sectors of the others are lacking the contractile-fibrillar layer over a certain length of their periphery. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 46. Cross-section. Posterior ring nerve (rn_2) of the somite with a nerve cell (nz) of the large tubes near the dorsal paramarginal longitudinal muscle strand. Longitudinal muscles (lm) and 2 free amoebocytes (am) of the mesenchyme are visible. Hermann's fluid, iron hemotoxylin. Scale: 450:1.

No, 47. Cross-section. Body wall. Typical skin epithelium (ep) with a gland cell (dz) at its highest functional phase; the most anterior ring nerve (rn_1) of the somite while the dorsal longitudinal muscle strand is traversing; the fibres (lm) of the latter show motoric nerve endings. The circular muscle fibre (am) accompanying the said nerve gives off lateral branches into the epithelium. Also visible are a diagonal muscle fibre and a free mesenchyme cell (am). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 48. Cross-section. Body wall at the lateral line of the body. Typical skin epithelium (ep) with a nearby pigment fat cell (pz); the nucleate cell sector of the circular muscle fibre (rmf) accompanying the anterior ring nerve (rn_1) with a process extending toward the epithelium; the lateral nerve (ln) is resting directly against this muscle fibre; diagonal (dm) and longitudinal (lm) muscles, part of the said ring nerve (rn_1), a free amoebocyte. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 49. Cross-section. Body wall. Circular muscle fibre (rm); diagonal muscle fibres (dm): between these some free amoebocytes (am) of the mesenchyme. The sensory nerve (sn) of the somite carries a small ganglion (gnz) anterior to the ventral intermediate longitudinal muscle strand (lm*). Longitudinal muscles (lm). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 50. Cross-section. Lateral ganglion (gnz) of the sensory nerve (sn) of the somite; the union of the said nerve with the lateral nerve (ln) is visible. Circular (rm) and diagonal (dm) muscle fibres, a free amoebocyte (am), longitudinal muscles (lm): below them the ventral paramarginal strand (lm*) one of whose cells is visible in the nucleate sector. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 51a, b. Cross-section. 2 successive sections. Body wall. Typical skin epithelium (ep) with gland cells (dz) in various functional phases. Circular (rm) and diagonal (dm) muscle fibres; longitudinal muscles (lm), in the middle their ventral paramarginal strand (lm*). The sensory nerve (sn) of the somite with which the lateral nerve (ln) unites. The lateral ganglion is divided into 2 parts (gnz). Free amoebocytes (am). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 52. Cross-section. Body wall. Typical skin epithelium (ep) with a gland cell (dz). The marginal lamella of the mesenchyme gives off some filaments (gl). Diagonal (dm) and longitudinal (lm) muscles; the ventral paramarginal strand (lm*) of the same. The posterior nerve branch (hnz) of the 4th somite annulus ends in the lateral nerve (ln). Free amoebocytes and a pigment fat cell (pz). Sublimate acetic acid, hemalum. Scale: 450:1.

Fig. 38

No. 53. Cross-section. Body wall. Typical skin epithelium (ep), circular (rm) and diagonal muscle fibres (dm). The lateral nerve (ln) gives off 2 nerve bundles which extend to the diagonal muscle fibres of the inner layer. Longitudinal muscles (lm), the lateral strand of these; one of its cells is visible in the nucleate sector. Pigment fat cells (pz) and free amoebocytes (am). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 54. Cross-section. Diagonal section through a chaetal sac. Only a medium-sized and a very small chaeta (bs) are visible in it; below its cells (bsz) are 2 large chaetae, 1 medium-sized chaeta, and 1 chaeta (bsz*) as in the skin epithelium. Visible laterally are muscle cells (mf) of the muscle apparatus of the chaetal sacs. The coelothelial coating with a well-developed cell (ct*). Hermann's fluid, iron hematoxylin. Scale: 450:1.

No. 55. Cross-section. A proximal chaetal end (bs); 3 chaetal sac cells (bsz), 1 of which (bsz*) is as in the skin epithelium, and 1 of which is very well-developed. In the protoplasm of the formative cell a finely-fibred cone coming from the chaetal end is visible. Hermann's fluid, iron hematoxylin. Scale: 450:1.

No. 56. Cross-section. Chaetal sac with a completely developed chaeta (bs) whose end is covered only by a very fine protoplasm layer of its laterally accumbent formative cell (bsz). Visible in addition to the large nucleus of the latter are a medium-sized (bsz*) and 2 small nuclei resembling the skin epithelium. A few muscle fibres (mf) have attached themselves to the proximal end of the chaetal sac which protrudes quite far into the coelom. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 57. Frontal section. Cross-sectioned chaetae (bs) and their sacs (bsz) in the ventral pair of the 1st head somite. Left: 2 diagonal muscle cells (mf*) of the respective muscle apparatus, right: cells (mf) inserting in the integument at the distal chaetal sac sectors. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 58. Cross-section. Diagonally-sectioned chaetal sacs in the lateral pair of the 5th head somite. The nuclei of their cells (bsz) are at various stages of development. Visible in one sac is only one small (bs*) chaeta, in the other sac a completely developed (bs) chaeta. Laterally are a diagonal cell (ms) of its muscle apparatus and an associated ganglion cell (gnz). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 59. Cross-section. Body wall at the dorsal median line in the anterior annulus of the 3rd head somite. Circular (rm) and longitudinal (lm) muscle fibres; in the inner body mesenchyme (ms) lies the 1st pair of eyes. Peripherally in the latter are pigment fat cells (pz) with protoplasm distincltly striated at one margin; in the centre are the retinal cells (rz) with inner bodies. In the coelom (c) are 2 muscle cells (mf*) coming from the supraesophageal ganglion mass. Visible laterally of one eye is the nerve associated with the latter (n). Sublimate acetic acid, hemalum. Scale: 450:1.

No. 60. Sagittal section. Eye of the anterior pair. Retinal cells (rz) with the light-refracting inner body that has radial striation peripherally. The pigment fat cells (pz) of the pigment cup are filled with black fat droplets and have a strongly pigmented proximal seam. Hermann's fluid, without staining. Scale: 450:1.

No. 61. Cross-section. The anterior body end. Because of the position of the 1st and 2nd head somites the section is slightly tangential in relation to these somites. Mainly the dorsal sectors of the latter are visible. Situated peripherally is the circular muscle layer (rm) whose fibres only give way to let the sensory papillae (sk) of the 2nd head somite pass through at the paramedian and intermediate line. The longitudinal musculature contains only the paramedian (pmd), intermediate (int), paramarginal (pmr) and lateral (lb) strands, each of which consist of only 2 muscle cells. Also visible are ends of the ventral, paramarginal and intermediate longitudinal muscle strands. Below are the sensory papillae (sk) of the 1st head somite, in the centre is a laterally sectioned muscle cell (mz) bending the lateral pair of chaetae of the 1st head somite from the inside. Posterior ring nerve (rn_2) of the 2nd head somite with a bipolar nerve cell: in the centre is one such cell of the anterior ring nerve (rn_1) of the same somite. Visible to the right and laterally is a part of the said nerve, while somewhat further down is a part of the posterior ring nerve (cn_2*) of the 1st head somite. Secretory ducts of the giant gland cells of the mesenchyme, and free amoebocytes. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 62. Frontal section. Cross-sectioned dorsoventral muscle cell (mz) of the 3rd head somite. Some muscle fibres (mf) have already separated from the nucleate cell sector. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 63. Frontal section. Initial sector of the intestine. The skin epithelium (ep), in which secretory ducts (aup) of the giant gland cells are visible, directly continues into the buccal cavity (mh). Here the latter is completely filled with the pharyngeal fold (phf) which has undergone a great anterior shift; this is followed by the pharyngeal sector (dph) into which the secretory ducts of the glands open. Visible in the pharyngeal wall is the epithelium and the mesenchyme layer (ms*) which directly merges with the mesenchyme (ms) of the body wall. In the mesenchyme of the fold are longitudinal muscle fibres (lm*)[1]; in the mesenchyme of the body wall are circular muscles (rm*), the muscles coming from the chaetae, and next to these the nerve (n*) which innervates the buccal cavity. The esophagus with its epithelium (oep), its circular (rm) and longitudinal (lm) muscle cells. In its mesenchyme layer are secretory ducts (aup) which enter here, coming from the esophageal mesenchyme lamella (ml). 2 anterior muscle cells (mz) of these are visible laterally above the esophagus, next to which 2 lateral vessels (qg_1) extend anteriorly in the coelom; also visible are a dorsoventral muscle cell (dvm_2) of the middle pair in the 2nd head somite, and proximally of it the eye nerve (n); posteriorly are the pharyngeal ring nerve at the level of the supraesophageal ganglion mass (obm), and finally muscle cells of the 2 anterior protractor pairs ($pc_{1,2}$). The coelom (c) enters the pharyngeal fold in the form of a narrow slit. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 200:1.

No. 64. Cross-section. The ventral half of the oesophagus. Its epithelium (oep), circular muscles (rm), and the mesenchyme layer (ms) with the longitudinal muscle fibres (lm); laterally is the posterior protractor pair (pc_1). Hermann's fluid, iron hematoxylin. Scale: 300:1.

No. 65. Sagittal section. Longitudinal section through the posterior sector of the esophagus. Its epithelium (oep), mesenchyme layer (ms), the gradually reducing circular musculature (rm), a longitudinal muscle fibre (lm), and coelothelium (ct). Sublimate acetic acid, hemalum. Scale: 550:1.

---

[1] The * has been omitted in the illustration.

No. 66. Cross-section. The left half of the esophagus in the plane of the stomodeal (sympathetic) ganglion (sgn). Visible in the middle are the epithelium (oep), circular muscles (rm) and in the mesenchyme layer (ms) longitudinal muscle fibres (lm); these are followed by the space that contains coelomocytes (cz), is coated with coelothelium (ct) and is delineated outside by the esophageal mesenchyme lamella (ml). In the latter are the stomodeal ganglion (sgn), the dorsal and ventral secretory duct cluster (aup), a circular muscle cell (mz), and 2 anterior protractors ($pr_{1,2}$). The outer coelothelial coating with an ordinary somatopleural cell (ct*). Sublimate acetic acid, hemalum. Scale: 400:1.

No. 67. Frontal section. The wall of the esophagus. Its epithelium (oep), circular (rm) and longitudinal (lm) musculature. Posteriorly of the esophagus protractors ($pr_{1,2}$) of the 2 anterior pairs and the mesenchyme lamella (ml) are given off in which are visible 2 thick circular muscle cells (mz), the stomodeal ganglion (sgn) and the associated nerve, and 2 secretory duct clusters (aup). In the coelom (c) are the lateral vessel (qg) of the 3rd pair and a dorsoventral muscle cell (dvm) of the inner pair of the 3rd head somite from which a few muscle cells have already separated. Sublimate acetic acid, hemalum. Scale: 300:1.

No. 68. Cross-section. The wall of the midgut whose epithelial cells (dep) are filled with droplets of a fat-like substance and whose nuclei are faintly visible. In some places in the mesenchyme layer (ms) such droplets are also visible, and the chloragogen cells (clz) are also filled with these basally as well as in the centre. In the coelom (c) are 2 coelomytes (cz) without such inclusions. Hermann's fluid, iron hematoxylin. Scale: 550:1.

No. 69. Frontal section. Epithelium of the hindgut in whose cells (dep) the fat-like droplets are embedded near the nucleus and basally. Hermann's fluid, iron hematoxylin. Scale: 450:1.

No. 70. Frontal section. The wall of the hindgut. The epithelial cells (dep) forming the folds contain only few fat-like droplets. They occur in the form of small clusters only proximally of the nucleus; basally they are only individually scattered. The intestinal blood sinus (ds) is completely without these, but they are quite numerous in the chloragogen cells (clz). Hermann's fluid, iron hematoxylin. Scale: 450:1.

Fig. 39.

No. 71. Cross-section. The wall of the hindgut. The tall gland epithelium (dep) forms folds corresponding to the position of the widest parts of the intestinal blood sinus (ds). The lamellae of the mesenchyme layer delineating the latter are particularly well visible on the longitudinal muscle fibres (lm). One such fibre is embedded in the mesenchyme strand (ms) extending from the inner to the outer intestinal sinus wall near the blood vessel. The dorsal blood vessel (dg) communicates openly with the intestinal blood sinus. Free blood cells (bz); in the coelom (c) near the intestine are a few chloragogen cells (clz). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 72a, b. Cross-section. Sections through the ventral blood vessel in a mid body somite. Externally is the coelothelium (cl), followed by the mesenchyme layer (ms), and internally is the inner layer (is) containing longitudinal muscle fibres (mf). A nucleate sector (is*) of a cell of the inner layer. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 400:1.

No. 73. Frontal section. The ventral blood vessel during its division in the head end. Visible below the coelothelium (cl) are the mesenchyme layer (ms) and the inner layer (containing no muscle fibres) with 2 nucleate cell sectors. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 74. A slightly oblique longitudinal section through a lateral vessel of the attachment disk, and

No. 75. cross-section of the same vessel whose wall consists only of the inner layer (is). The nucleate sectors of the latter protrude far into the blood vessel cavity (gh). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 300:1.

No. 76. Cross-section. The dorsal blood vessel in a somite of the midgut region. Below the coelothelium (ct) the vascular wall consists only of the mesenchyme layer (ms). The coelothelial coating with a typical cell (ct), haemocytes (hz) and a coelomocyte (cz). Sublimate acetic acid, hemalum. Scale: 400:1.

No. 77. Cross-section. The dorsal blood vessel in one of the posterior head somites. Visible below the coelothelium (c) are the external mesenchyme layer (ms) with an amoebocyte (am) folowed by the circular muscle layer (rm) and finally the inner membrane (is) with the nucleate sector of its cell (is*). In the vessel is a haemocyte (hz). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 78a, b. Cross-section. 2 successive sections of the anterior nephridial leg in the mid body. Left: a cell (npz_1) of the nephridial section with ramified tubules of which some rami are visible; right: a cell (npz_3) of the sector anterior to the sector extending to the skin epithelium invagination. At first separate, then resting closely against the other cells is the nephridial sector (npz_2) which ventrally unites the anterior and posterior nephridial legs. In Fig. 78c the said sector merges with the corresponding sector (npz_2) of the anterior leg. 2 cells of this sector are visible in the section which is 4 sections apart from the previous one. Hermann's fluid, iron brazilin. Scale: 300:1.

No. 79. Cross-section. Longitudinal section through the dorsomedian nephridial sector. 2 closely accumbent cell cords with the corresponding nuclei and central canals. Sublimate acetic acid, hemalum. Scale: 300:1.

No. 80. Cross-sectionw. Section through the posterior nephridial leg. The nucleate sector belongs to the cell (npz_3) of the section closest to the nephridial opening. Hermann's fluid, iron brazilin. Scale: 300:1.

No. 81. Cross-section. Section through the nephridial sector anterior to the skin epithelium invagination. Hermann's fluid, iron brazilin. Scale: 300:1.

No. 82. Cross-section. The rudimentary nephridium of the 3rd clitellar somite. At the apex of a typical skin epithelium invagination (ep) is only a single cell (npz) of the excretory nephridial sector. Circular (rm) and diagonal (dm) muscle fibres; longitudinal musculature (lm) in which the ventral intermediate strand (lm*) is visible; the end of a diagonal muscle cell (mf); free amoebocytes of the mesenchyme. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 300:1.

No. 83. Cross-section. Part of a section through the 1st clitellar somite. The typical epithelium (dep) of the midgut forms longitudinal folds; under these in the mesenchyme layer (ms) are longitudinal muscle fibres (lm); these are followed by the coelom sector surrounding the intestine which only dorsally forms a well-defined sinus (c) with the chloragogen cell layer (clz) at the intestine; over the remaining distance, the coelom is tightly packed with coelothelium cells (ct*) which protrude laterally at the lateral line of the intestine in the form of a botryoidal mass (h_1) into the lumen of the testis to form its spermogenetic zone. The inner body mesenchyme (ms*) is bordered on one side by the coelothelial membrane of the coelom (ct) and on the other side by that of the testis (ct_1). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 84. Cross-section. Same as in the previous illustration, but a smaller part of the section is shown. The spermatogenetic zone (h_1) occupies a longer piece, and some of its cells completely separate from the rest of the mass. Sublimate acetic acid, borax carmine/indigo carmine. Scale: 450:1.

No. 85. Cross-section. Same as in the previous illustration, showing an even smaller part of the section. Visible are a mesenchyme strand (ms_1) connecting the inner body mesenchyme (ms*) with the mesenchyme layer of the intestine (ms). A cell (sz) of the spermatogenetic zone (h_1) of the testis lies freely in the cavity of the latter; it is a spermatocyte of the 1st order. Sublimate acetic acid, hemalum. Scale: 550:1.

No. 86. Cross-section. A nutritive (ncz) cell of the testis surrounded by the mass of spermatocytes (sz) of the 1st order; laterally are separated cytophores (cy). Sublimate acetic acid, borax carmine/indigo carmine. Scale: 300:1.

No. 87. Cross-section. Edge of the sperm funnel. The coelothelial coating (ct) of the testis suddenly merges with the epithelium of the gonostome (st) on which a group (st*) of separating cells lies near the edge. Sublimate acetic acid, hemalum. Scale: 450:1.

No. 88. Cross-section. The wall of the atrium of the male reproductive apparatus. The typical gland epithelium (dz) of the atrium between whose cells lie a few filament-shaped elements (ep) with nuclei as in the skin epithelium. In the thin mesenchyme layer are circular muscle fibres (mt). Sublimate acetic acid, hemalum. Scale: 250:1.

No. 89. Cross-section. The wall of the ovisac at the transition between the vertical and the horizontal sector. At the basis of the typical epithelium (ovp) of the ovisac are longitudinal muscle fibres (mf); visible in the mesenchyme layer (ms) below the coelothelial coating (ct) are undifferentiated cells (edz) which originated in the coelom gland. Sublimate acetic acid, hemalum. Scale: 300:1.

No. 90. Cross-section. Horizontal sector of the ovisac. Belonging to its wall: outside the coelothelial layer (ct), in the middle the mesenchyme layer (ms) with a circular muscle cell (rm) and a longitudinal muscle fibre bundle (lm), inside the epithelium (ovp) of the ovisac. In the lumen of the latter is a nutritive cell (ncz) against which a mass of ovocytes is resting. Sublimate acetic acid, hemalum. Scale: 300:1.

No. 91. Cross-section. The posterior end of the ovisac. The layers of the coelothelial (ct) and inner (ovp) ovisac epithelium can hardly be differentiated from each other. Between them in the mesenchyme layer (ms) are 2 groups of differentiating circular muscles (rm) of the ovisac wall; bundles of longitudinal muscle fibres (lm); in the centre are the developing egg cells (oc). Sublimate acetic acid, hemalum. Scale: 300:1.

Fig. 40

No. 92. Cross-section. Ventral median part of a section taken at the boundary between the 2nd and 3rd clitellat somite. Fig. 34, No. 9 is a half schematic view of the same section. In the middle is the coelom gland (cd) of the female reproductive apparatus. Its ventral part protrudes into the posterior cavity (ah) of the female reproductive apparatus as a conspicuous mass; here the coelom gland is covered with a coelothelial coating (ct_1); 2 cells of the same are visible in the section; it is sometimes interrupted; the cells (cz) separating from the coelom gland in such places lie freely in the posterior cavity. The latter is lined with coelothelium (cz); at its wall a muscle fibre (mf*) lies in the inner body mesenchyme; ventrally the said cavity enters between the longitudinal muscles (lm), a bundle of which (lm*) even extends freely into the cavity; here the coelothelial coating (ct) is peculiarly changed. Below it are many amoebocytes (am) in the mesenchyme (ms) of the body wall. Visible are longitudinal (lm), diagonal (dm), and circular (rm) muscle fibres of the body wall, laterally a pigment fat cell (pz) and a secretion duct cluster (aup) of the giant gland cells. The typical skin epithelium (ep) forms an invagination at the median line, the spermatheca (spt) at whose apex the processes (mf_1) of the 2 ventral dissepiment muscle cells (dsz_1) traversing the posterior cavity attach themselves. The upper part of the coelom gland forms the basal sector of the ovisac (ov). Between its cells extend longitudinal muscle fibres (mf) of the latter; the inner muscle cell (mz) generating them is visible in the mesenchyme surrounding the intestine. Between both parts of the coelom gland lies a mesenchyme layer (ms_1). Top: the ventral coelom sinus (c_1) with the ventral blood vessel (vg) and the connective (cn) of the ventral cord. Sublimate acetic acid, hemalum. Scale: 250:1.

No. 93. Schematic representation of the anterior section of the reproductive apparatus (top view). Next to the lateral line is the voluminous sac-like testis (h) which begins at the boundary between the 3rd preclitellar (8) and 1st clitellar (9) somite. In the middle of the latter somite lies the spermatogenetic zone (h_1) at the medial wall of the testis.

Visible at the boundary between the 1st (9) and 2nd (10) clitellar somite is the sperm funnel (st) which then merges with the sperm duct (vd) and the ejaculatory duct (de); the latter leads into the atrium (at) which openes externally through the male genital pore (ø). The central sector of the female reproductive apparatus is formed on each side by a coelom gland (cd) that protrudes ventrally into the posterior cavity (ah) of the said apparatus, merges dorsally with the basal sector of the ovisac (ov) and slightly protrudes anteriorly into the upper part of the sector (ut) discharging the reproductive products. The discharge duct opens externally through the female reproductive pore (↓) between the 3rd and 4th annulus of the 2nd (10) clitellar somite. At the boundary between the 2nd (10) and 3rd (11) clitellar somite is the spermatheca (spt).

No. 94. Schematic representation of the reproductive apparatus, anterior sector (top view). Right and left: 2 voluminous testes (h) beginning at the boundary between the 3rd preclitellar (8) and the 1st clitellar (9) somite. In the middle of the latter somite is the spermatogenetic zone (h_1) at the medial wall of the testis. At the boundary between the 1st (9) and 2nd (10) clitellar somite is the sperm funnel (st) which merges into the sperm duct (rd) and then into the ejaculatory duct (de) of the respective side. Dorsally the ejaculatory ducts lead into the atrium (at) of the male reproductive apparatus; the atrium opens externally through the male pore (ø). Visible in the female reproductive apparatus are 2 coelom glands (cd) which protrude into the posterior cavity (ah) of the apparatus, and enter anteriorly into the proximal part of the sector discharging the reproductive products (ut); dorsally these glands represent the basal sectors of the ovisacs (ov).

No. 95. Schematic representation of a nephridium in the mid body. The anterior nephridial leg consists of 3 cell cords: one of these (npz_1) contains a system of branching tubules, while each of the other two (npz_2, npz_3) contain only an unbranched central canal. The posterior nephridial leg is also formed of 3 cell cords (npz_1*, npz_2*, npz_3*) which represent a continuation of the cell cords of the anterior leg: they each contain only one unbranched central canal. The dorsomedian nephridial sector (dmt) contains 2 cell cords. Also visible are 2 connecting cell cords, one at the lateral line of the intestine, the other ventrally. Skin epithelium invagination with the approaching nephridial cord.

No. 96. Schematic representation showing the position of each nephridial sector in relation to the other organs in a mid body somite. Shown is a cross section of the body in the region of a dissepiment. Typically developed body wall; ventrally at the intermediate line is the skin epithelium invagination of the nephridium. In the inner body mesenchyme are the testis (h) and the giant gland cells (gdz). The coelom is represented only by the dorsal (c) and ventral (c_1) dissepiment opening. In the former the ovisacs (ov) and the blood vessel lie quite freely; the other contains the connective (cn) of the ventral cord and the ventral blood vessel which has the dorsal sector of its mesentery. In the plane of the section only the anterior (darker coloured) nephridial leg is visible which lies near the intestine in the mesenchyme. The posterior leg and the excretory nephridial sector (shown in a lighter colour) are already outside the plane of the section, further caudad (in the 1st annulus of the somite following the illustrated dissepiment). The dissepiment muscle cells are not included in the illustration. Scale: 75:1.

No. 97. Schematic representation of a neurosomite in the mid body. The connective (cn) and a ganglion (gn) of the ventral cord. The 2 motoric ring nerves coming from the latter, the anterior (rn_1) and posterior (rn_2) and the middle sensory nerve (sn) of the somite. Nerve cells (nz) of the large tubes on the ring nerves and ganglion cells (gnz), on all 3 nerves (on the ring nerves only at the lateral line). Dorsal nerve (dn). In the 2nd somite annulus (II) are the groups of sensory papillae (sk). The lateral nerve (ln) which communicates with all 3 nerves of the somite and with a nerve branch (hnz) in the 4th somite annulus (IV). The dorsal and ventral longitudinal muscle strands (pmd, pmd_1, int, int_1, pmr, pmr_1) and the lateral strand (lb) which closely communicate with the ring nerves.

No. 98. Cross-section. Half schematic representation of a section through the connective of the ventral cord. The 2 connective trunks (cn*) and the median nerve cluster (mn). In the mesenchymatous neurilemma layer are longitudinal muscle fibres (mf); externally lies the coelothelial coating (ct). Scale: 550:1.

Fig. 99. Cross-section. Half schematic representation of a cross section through the ganglion of the ventral cord. A median ganglion cell follicle (mp) and 2 lateral follicles (lp); the central fibre mass (cfm) of the ganglion with nerves (n) extending vertically ventrad from it. Visible in the mesenchymatous neurilemma sheath of the ganglion are 2 muscle fibres (mf). The external coelothelial coating (ct). Scale: 300:1.

No. 100. Frontal section. Half schematic representation of a frontal section through a ganglion of the ventral cord in which are visible 2 median ganglion cell follicles [an anterior (mp_1), and a posterior (mp_2)] and 2 pairs of lateral follicles [an anterior (lp_1) and a posterior (lp_2)], as well as the departure points of the anterior (n_1), middle (n_2) and posterior (n_3) nerves. Scale: 500:1.

Fig. 41

No. 101. Schematic representation of the innervation of the head region. The 5th (7) head somite innervated by the 1st ordinary ganglion (gn_5) of the ventral cord, with 2 ring nerves [an anterior ($rn_{5(1)}$) and a posterior ($rn_{5(2)}$], and a sensory nerve (sn_5); the branch (hnz_5) for the 4th somite annulus. The 4 other head somites (1-4) are innervated by the 4 respective ganglion systems of the subesophageal ganglion mass. The 4th somite (4) contains 2 nerves, one of which (n_4) gives rise to the posterior ring nerve ($rn_{4(2)}$) with the branch (hnz_4) for the 4th somite annulus and the sensory nerve (sn_4), while the other (n_4*) represents the anterior ring nerve ($rn_{4(1)}$). The 3rd head somite (3) is supplied by a single nerve (n_3) which forms the anterior ($rn_{3(1)}$) and the posterior ($rn_{3(2)}$) ring nerves with the branch (hnz_3) for the most posterior sector of the somite and the sensory nerve (sn_3). The 2nd head somite (2) has only 2 nerves, namely a posterior ($rn_{3(2)}$) and an anterior ($rn_{3(1)}$) ring nerve which are formed by the 2nd nerve (n_2) of the subesophageal ganglion mass. Their 1st nerve (n_1) extends into the 1st head somite (1) where it forms 2 poorly developed ring nerves ($rn_{1(2)}$, $rn_{1(1)}$). The pharyngeal connectives give off 2 nerves, one of which (an_1) extends to the eye which is situated on the dorsal median line in the 3rd head somite, the other (n*) represents the stomodeal nerve which divides into 2 branches (one leading to the buccal cavity, the other to the esophagus). The supraesophageal ganglion mass does not directly give off any nerves. Lateral nerve (ln), sensory organs (sk). For the sake of clarity, the individual somites are presented without their dorsal curvature, i.e. as completely vertical rings. The eyes of the 4th and 5th somites are not shown.

No. 102. Schematic representation of the subesophageal and supraesophageal ganglion masses (ventral, slightly frontal view). On each side above the pharyngeal connectives (scn) 6 ganglion cell follicles form the supraesophageal ganglion mass (obm). Each pharyngeal connective gives off 2 nerves, one (n) extends to the eye of the 3rd head somite, the other represents the stomodeal nerve (n*). The subesophageal ganglion mass consists of 4 ganglion complexes. Each corresponds to an ordinary ganglion of the ventral cord and contains 2 ventral median ganglion cell follicles (mp_1 mp_2, mp_3, mp_4) and 2 pairs of lateral (lp_1 lp_2, lp_3, lp_4) follicles. The posterior ganglion complex of the subesophageal ganglion mass gives off 2 nerves on each side (n_4, n_4*), while the remaining 3 give off only one nerve on each side (n_3, n_2, n_1).

No. 103. Schematic representation of the blood vascular system in the head region. Visible are the dorsal vessel (dg) with the 5 lateral vessels it gives off (qg_{1-5}); the ventral vessel is hidden by the esophagus (oe).

No. 104. Schematic representation of the blood vascular system in the posterior body end. The light-red ventral blood vessel (vg) gives off 4 pairs of lateral vessels (qg_{1-4}). The deep-red dorsal vessel (dg) divides at the boundary between the 5th (24) and 6th (25) somite of the hindgut region. After entering the inner body mesenchyme at the most posterior body dissepiment, each of the two thus formed vessels give off 4 lateral vessels (qg_{1-4}). The 2 middle vessels ($qg_{2,3}$) have a common root, and the left most posterior vessel (qg_4) originates only from the vessel (dg) originating in the union of the two said branches behind the intestine. Between the latter an anastomosis is visible. The 4 pairs of ventral and dorsal lateral vessels unite in pairs at the edge of the attachment disk; the vessels representing the continuation of the dorsal and ventral blood vessel, respectively, also merge on the median line of the body. The thus formed 9 vessels communicate with each other at the edge of the attachemnet disk through the ring-shaped blood vessel (rg).

No. 105. Schematic representation of the anal ganglion mass (ventral view). The ganglion cell follicles (mp_1, lp_1) of the 1st system that corresponds to an ordinary ganglion of the ventral cord are arranged in typical fashion. In the 3 following systems the lateral follicles ($lp_{2,4}$) of the anterior pair gradually shift dorsad in comparison with those of the posterior pair; the median follicles arrange themselves either at a certain angle to each other (mp_{2-3}) or symmetrically on each side of the median line of the body (mp_4). In the most posterior ganglion system the median follicles are hardly separated from the posterior lateral follicles, and the same applies to one side of the 3rd system (mp_3, lp_3). Laterally 2 nerves (n_1) are given off on each side by the 1st ganglion system, while the other systems each give off only one nerve (n_2 1_1) in their anterior sector; also visible is a pair of nerves (n*) forming the ends of the connective trunks (cn).

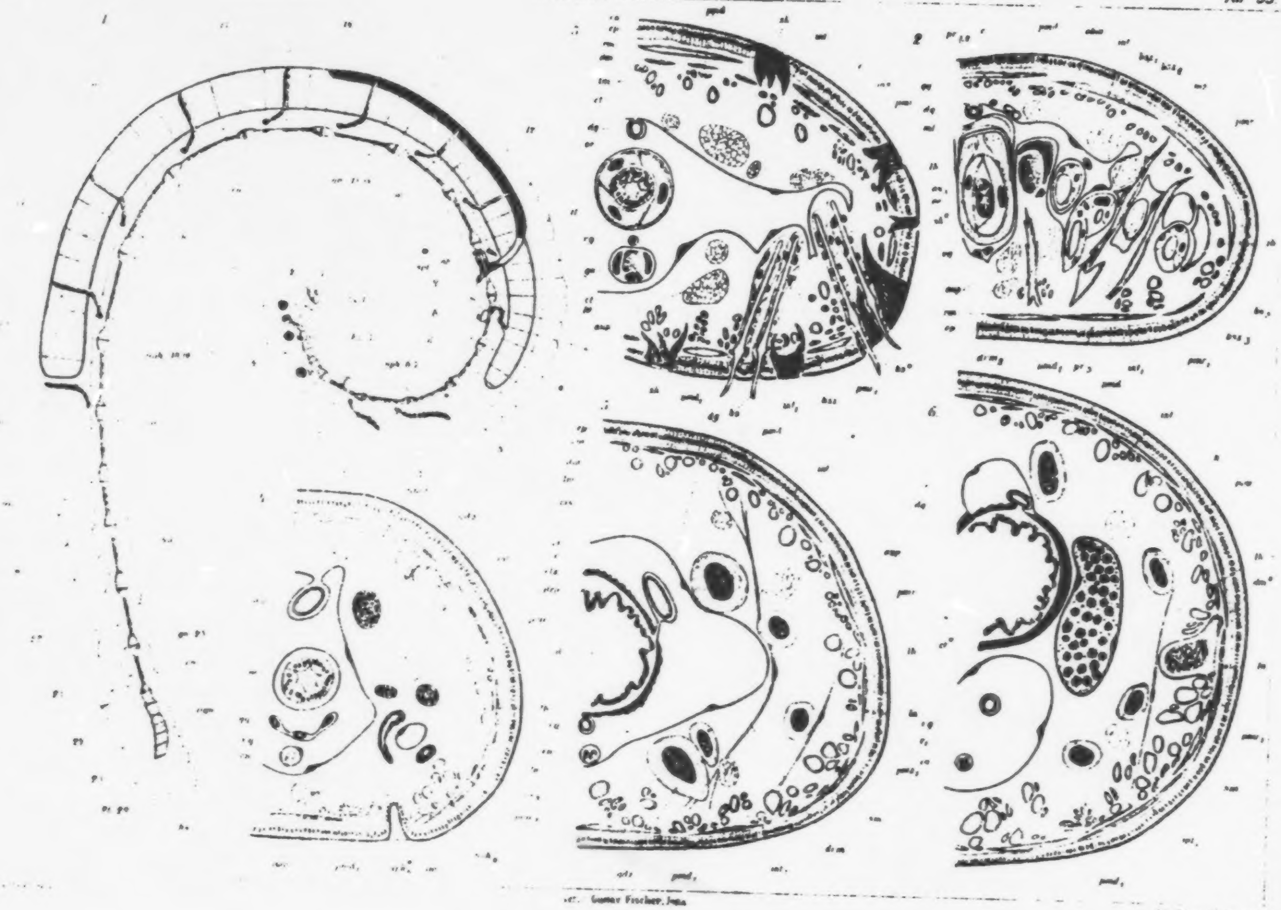
No. 106. Schematic representation of the coelom in the 5th body somite, the 3 preclitellar somites (6-8) and the 1st clitellar somite (9). Frontal section approximately at the level of the lateral line of the body. The coelom of the 2nd (c_7) and 3rd (c_8) preclitellar somites forms outpouchings (cs_{7-8}) extending cephalad between the coelom wall of the previous somite and the longitudinal muscles of the same. The 1st preclitellar somite contains no such outpouchings; its coelom (c_6)

communicates directly with the following coelom sinus (c_5) of the 5th head somite, since the respective dissepiment (dsp_5, shown in the illustration) consists of only one ventral muscle arc. The coelom of the 1st clitellar somite (9) is densely packed with coelothelium cells (clz) which in one place (h_1,) protrude directly into the testis (h). The intestine (d) - except the esophagus (oe) - is covered by the chloragogen cells (clz).

No. 107. Half schematic frontal section of the posterior body end, showing the contours of its somite annuli and the hindgut (hd). Note the coiled course of the latter and its division into sectors (hd_{1-6}) corresponding to the body somites (20-25). Scale: 50:1.

No. 108. Schematic representation of the posterior body end. It shows the outline of a part of the midgut (d), of the hindgut (hd), and the endgut (an). Blood vascular system: the intestinal blood sinus which exists only in the hindgut is shown light-red; the dorsal (dg) and ventral (vg) blood vessels are deep-red. They communicate with the blood sinus - the ventral vessel through 5 vessels traversing the dissepiments (dsp_{20-24}), and the dorsal vessel through several open connections in each somite. The coelom is stained black and visible in its ventral and dorsal sectors. The dissepiments (dsp_{19-25}) which separate the metameric coelom sectors (c_{19-25}) from each other have been shifted cephalad in comparison with the corrseponding sectors of the body wall (19-29). The most posterior coelom sac (c). Beginning parts of lateral vessels at the ventral and dorsal blood vessels: ring-shaped vessel (rg) of the attachment disk.

Fig. 33

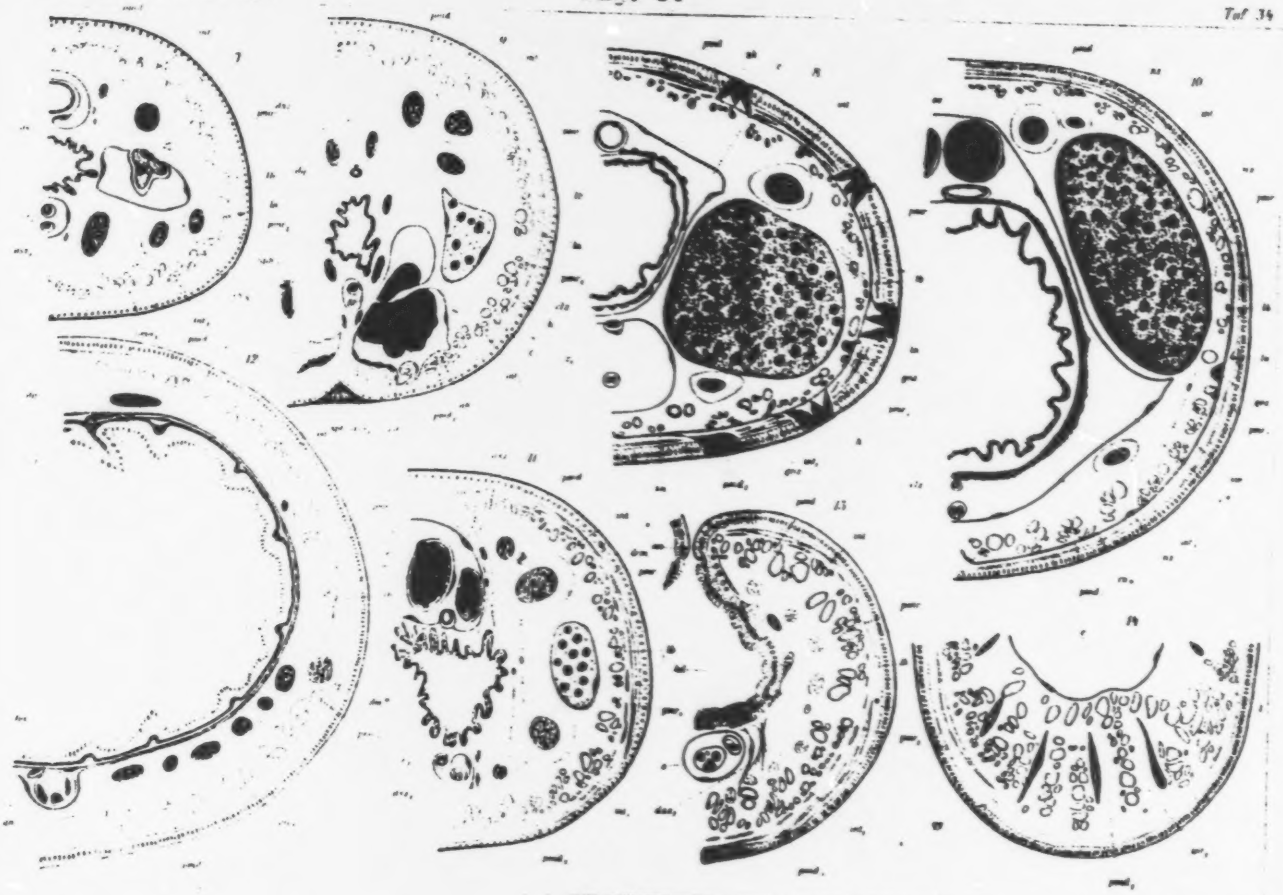

1
2
6
pmd₁
ent₁
dvm
pmd₁

Gustav Fischer, Jena

Zoolog. Jahrbücher Bd. 22 Abt. f. Morph.

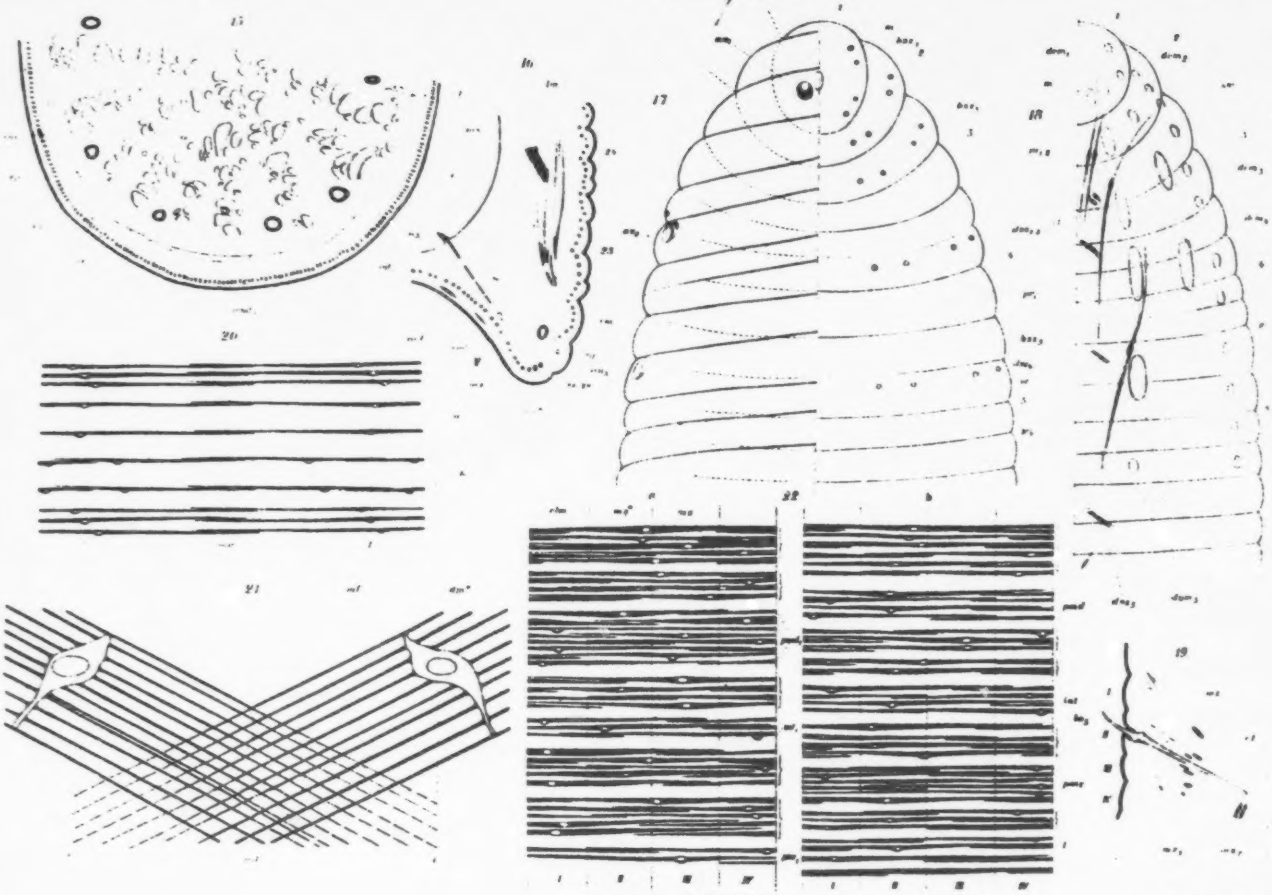
Fig. 34

Taf. 34


7
8
9
10
11
12
13
14

Verl. v Gustav Fischer, Jena.

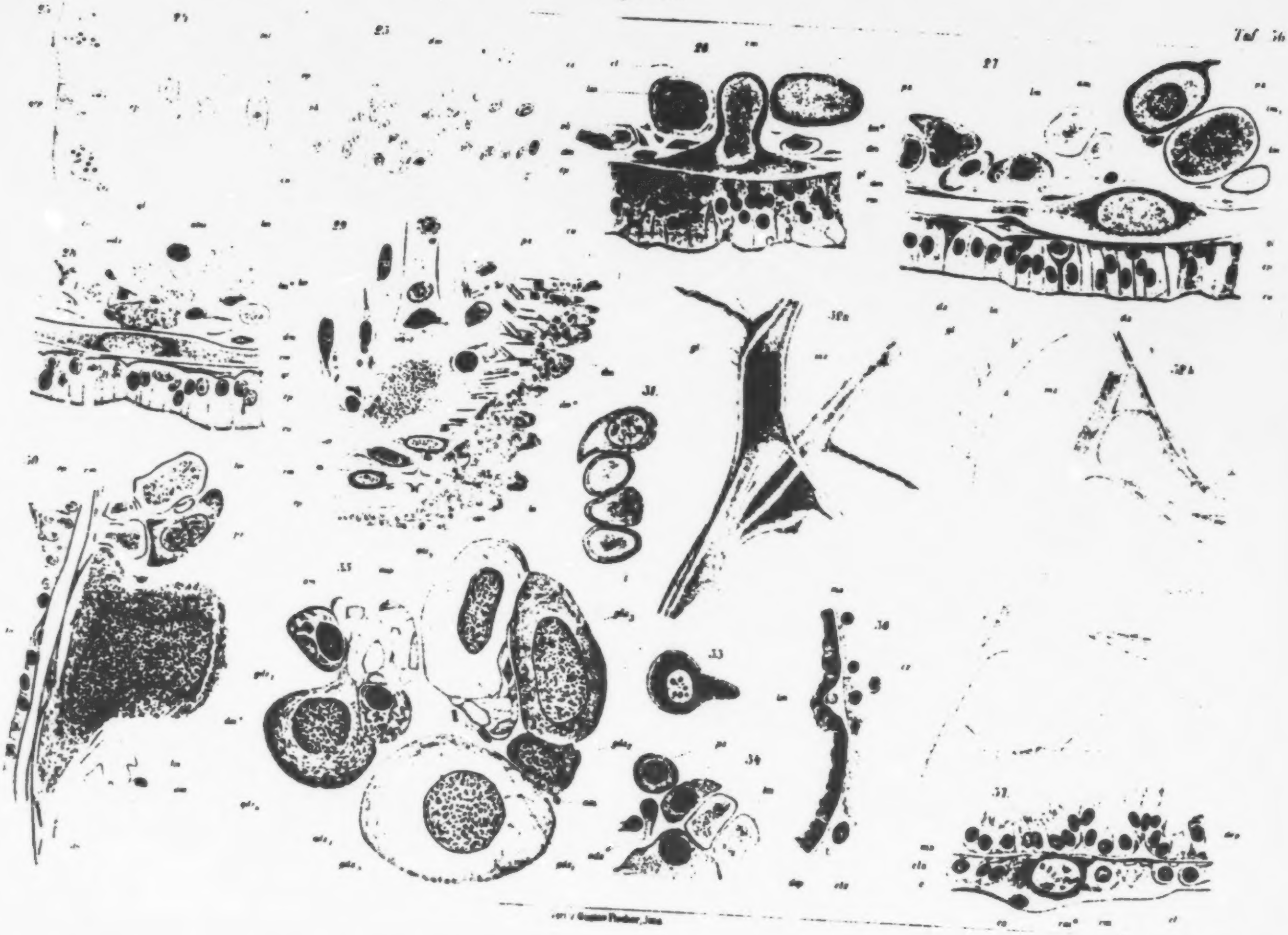
Fig. 35 eye


15
16
17
18
19
20
21
22
a
b
I
II
III
IV
dm
bas
dom
pm

Gustav Fischer, Jena

Zoolog. Jahrbücher Bd 22 Abt. f. Morph.

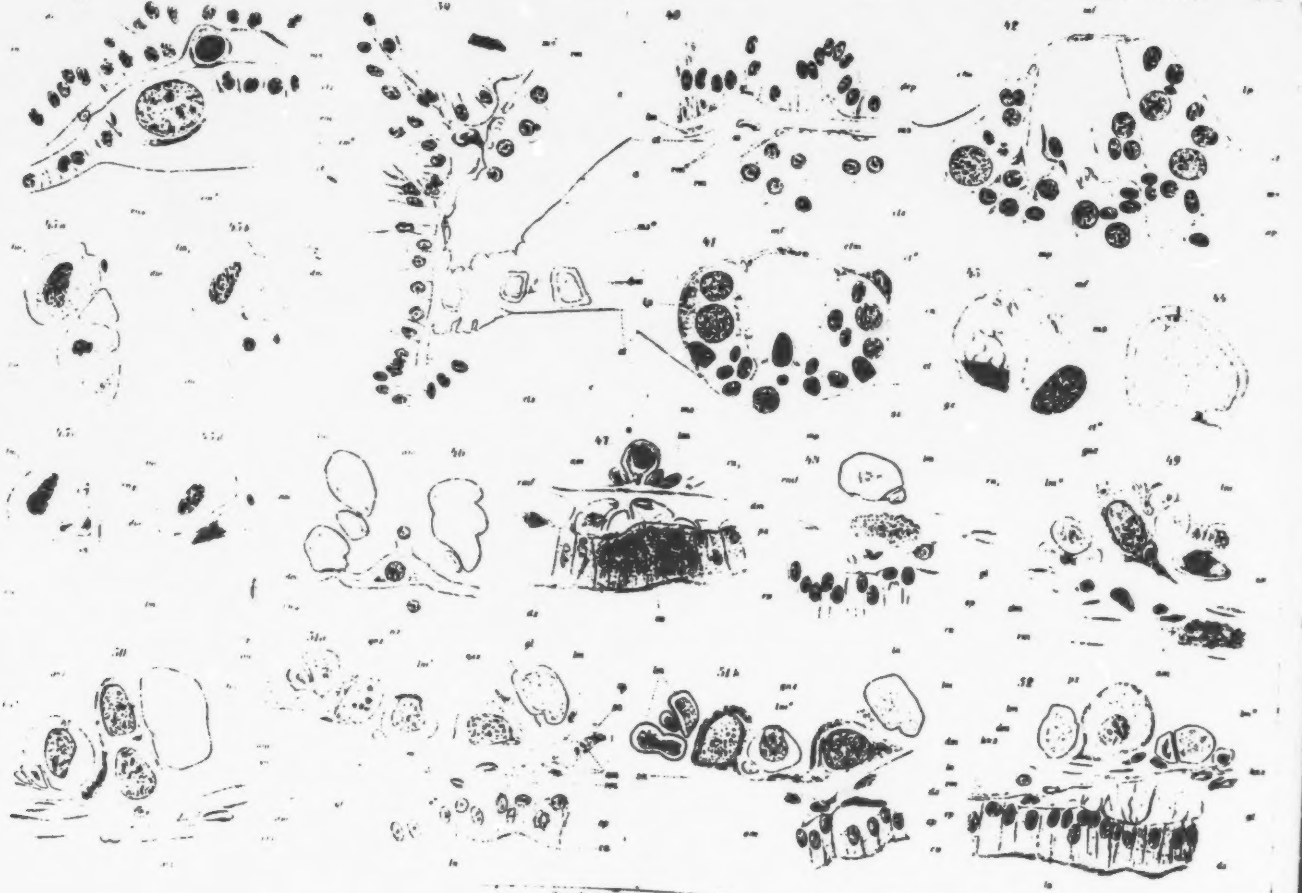
Fig. 36


Taf. 36
25
26
27
28
29
30
31
32a
32b
33
34
35
36
37

[illegible] Gustav Fischer, Jena

266

Fig. 37

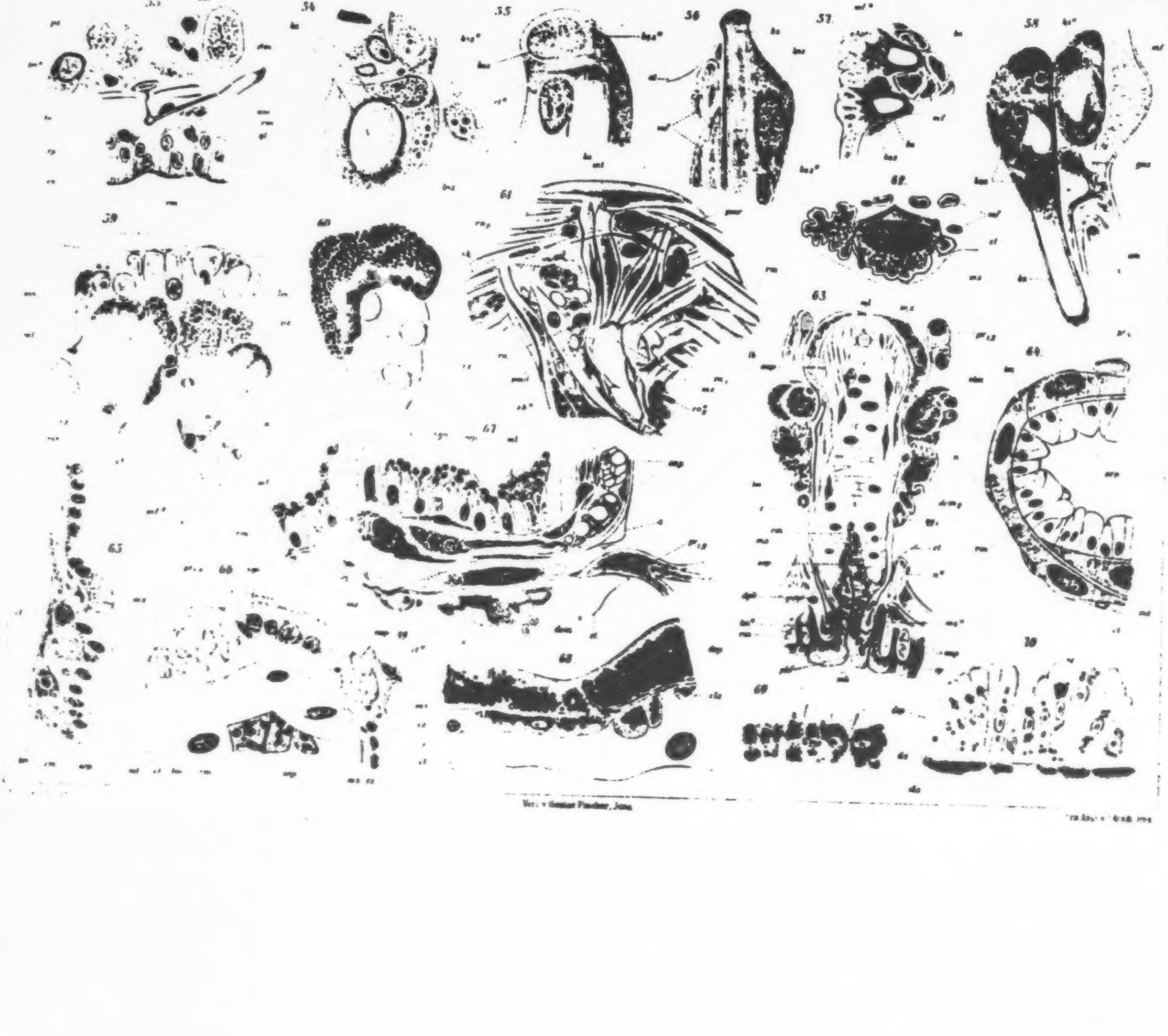

38
39
40
41
42
43
44
45a
45b
45c
45d
46
47
48
49
50
51a
51b
52

Verl. v Gustav Fischer, Jena

Lith. Anst. v. A. Giltsch, Jena.

Zoolog. Jahrbücher Bd. 22. Abt. f. Morph.

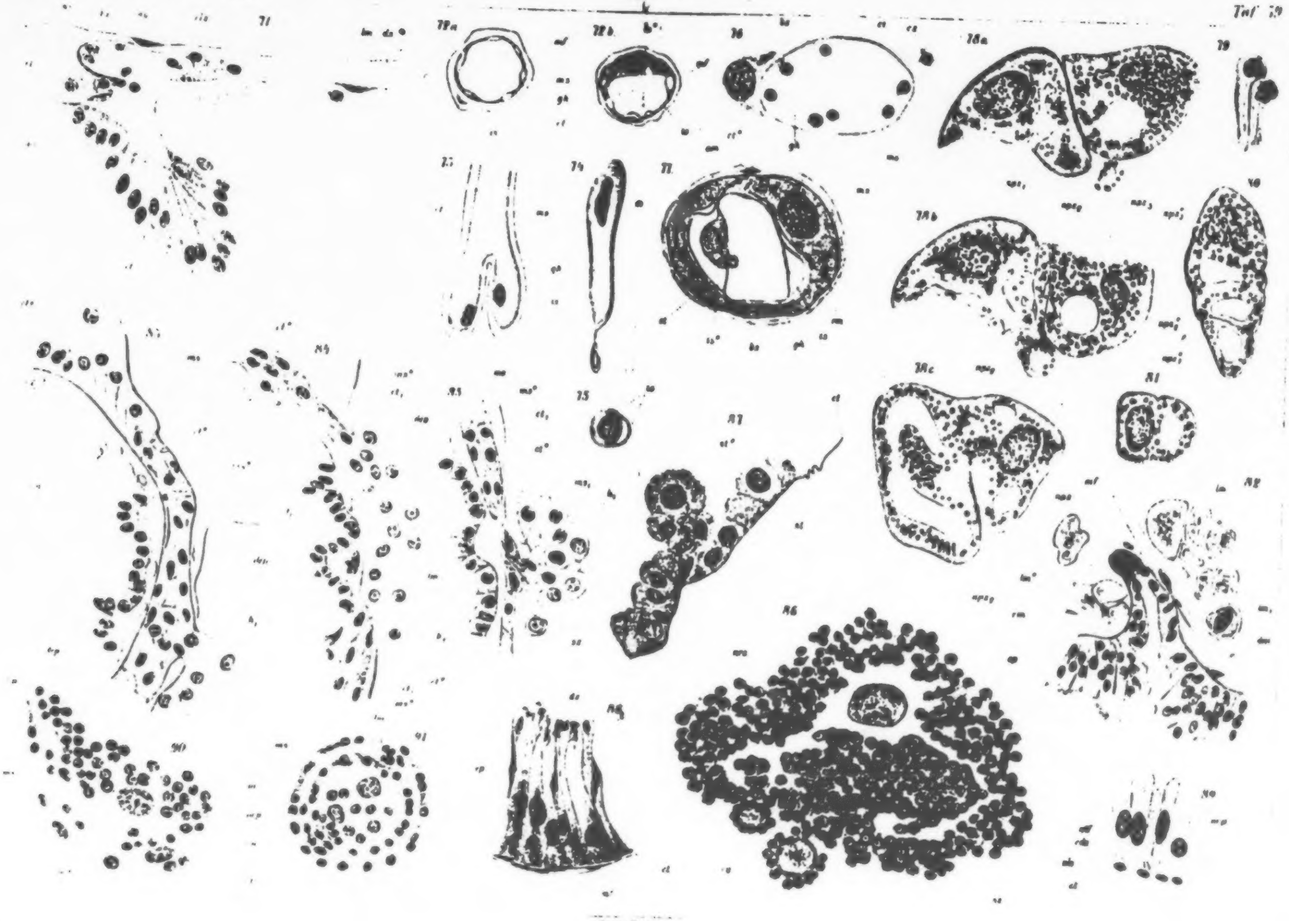
Fig. 38


53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70

Verl. v. Gustav Fischer, Jena.

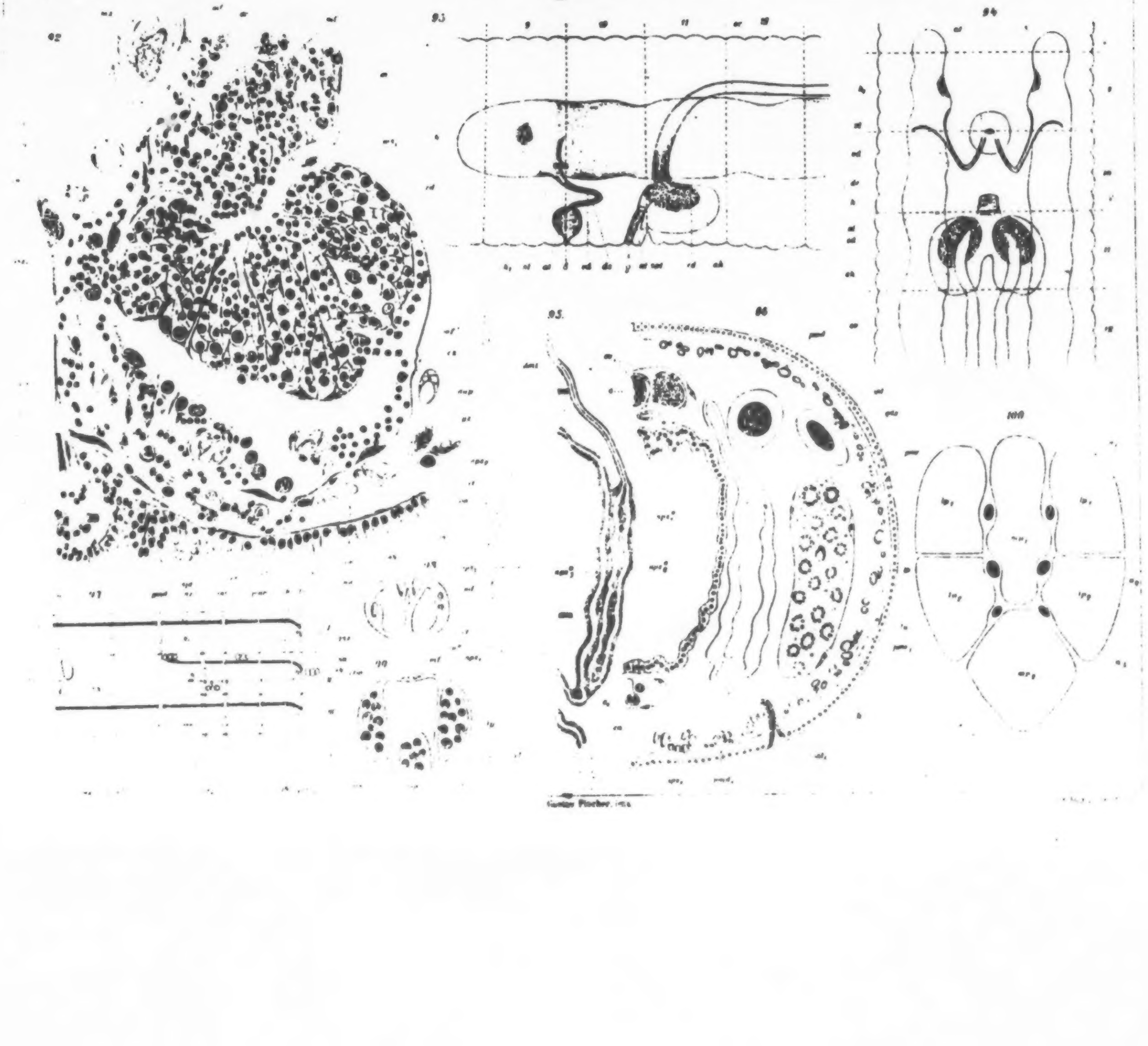
Lith. Anst. v. J. Arndt, Jena

Fig. 39


71
72a
72b
76
78a
79
73
74
77
78b
80
78c
81
85
84
83
75
87
82
86
90
91
89
ms
ep
ct

Gustav Fischer, Jena

Fig. 40

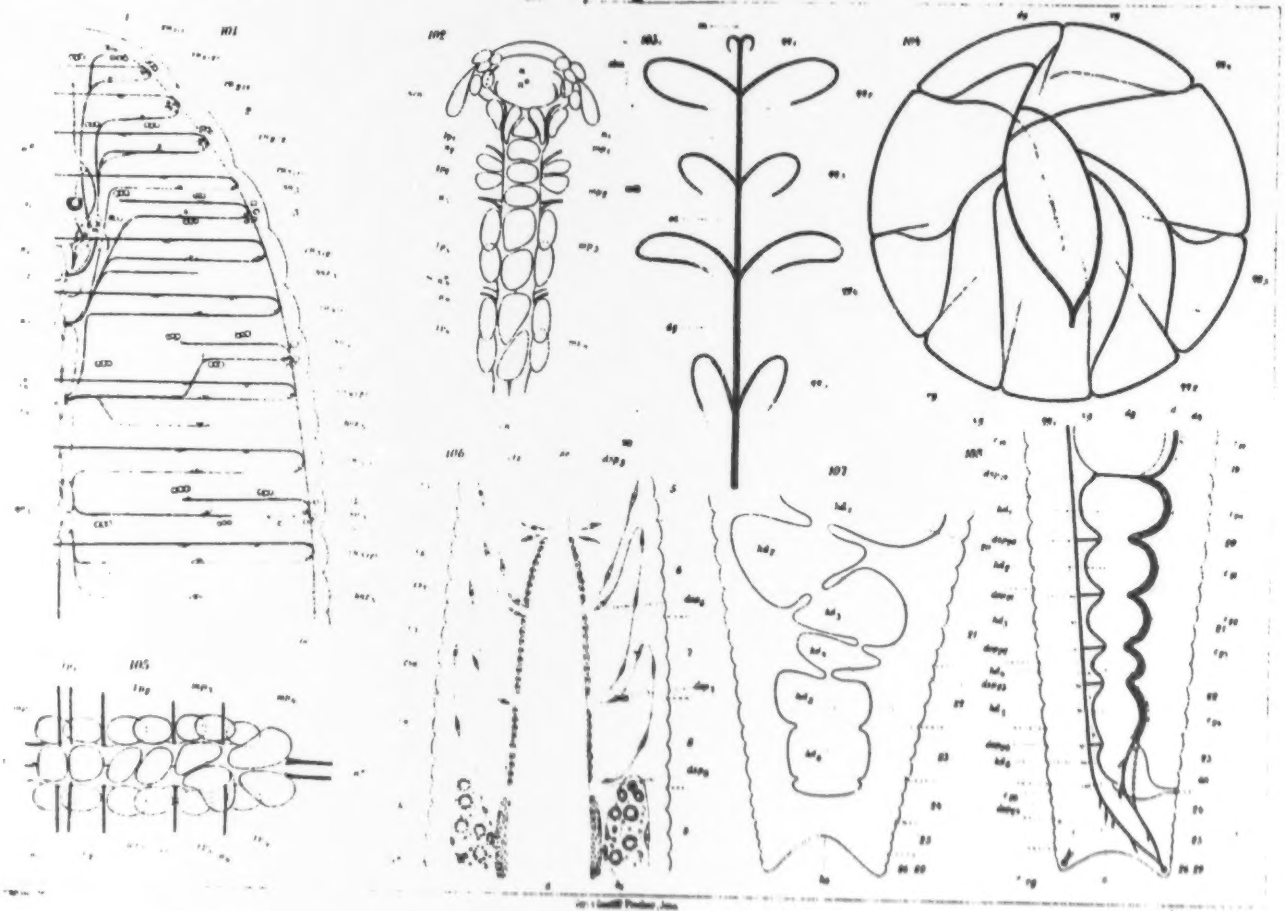

92
93
94
95
96
97
99
100
Gustav Fischer, Jena.

270

Fig. 41

Zoolog. Jahrbücher Bd 22. Abt. f. Morph.

Taf. 41


101
102
103
104
105
106
107
108

Verlag v. Gustav Fischer, Jena.